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CONTENTS

The Water Exchanges of Some Small Mammals

ROBERT M. CHEW

(Pp. 215-225)

Vegetation and Habitats in a Southwestern Volcanic Area

ALTON A. LINDSEY

(Pp. 227-253)

Studies on Plant Succession in True Prairie

LOREN W. MENTZER

(Pp. 255-267)

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THE WATER EXCHANGES OF SOME SMALL MAMMALS¹

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	215	PROCEDURE	218
MATERIAL STUDIED.....	215	RESULTS	219
METHODS	216	Water Drunk	219
General	216	Free Water in the Food, Water of Oxidation....	219
Water Drunk.....	216	Urinary and Fecal Water Loss.....	219
Free Water in the Food.....	216	The Insensible Loss of Water.....	220
Urinary and Fecal Water Loss.....	216	Response to Restriction of Drinking Water Supply	222
Respiratory Exchanges.....	216	DISCUSSION	223
Water of Oxidation.....	217	SUMMARY AND CONCLUSIONS.....	224
Insensible Water Loss.....	217	LITERATURE CITED.....	224
Modifications for Blarina.....	217		

INTRODUCTION

Animals are continually exchanging water with their environment. Water is taken from the environment as water drunk, as free water in the food eaten, and as the water of oxidation potentially present in the foodstuffs. Water is lost to the environment in the urine and feces and by evaporation from skin and lung surfaces. From day to day, intake may exceed loss, or vice versa, but in the long run an animal must be in water-equilibrium with its environment, and the equilibrium must be at a level adequate for the normal maintenance of protoplasm.

The factors which determine the availability of water to and the loss of water from a mammal vary distinctly from one habitat to another. Such differences can be expected to influence distribution and abundance of mammals and are matched by physiological and behavioristic adaptations by the mammals. Also there can be expected to be differences in the water-requirements of different species.

The present work follows three courses: (1) measurement of the water-exchanges of certain small mammals as they occur under environmental conditions normal to the animal, providing food and water ad libitum, (2) measurement of the water exchanges under conditions foreign to the animal, (3) measurement of the exchanges occurring when the water supply is severely limited. The purpose of the first course is to demonstrate any inherent differences in the level of equilibrium for mammals from different habitats, while the second and third courses will expose any adaptations and limitations of the water-exchange mechanism.

A few studies of the water habits of small mammals have been made. Dice (1922) was not able to find any differences for food and water intake, or temperature and humidity tolerance, between the prairie and woodland deer mice, *Peromyscus maniculatus bairdii* and *P. leucopus noveboracensis*. Johnson (1926) found that *P. l. noveboracensis* did not react positively to conditions of low evaporation, which may be expected to exist in their woodland habitat.

Ross (1930) found a significant difference between the water drinking habits of *P. maniculatus* and *P. eremicus*, but not between subspecies within either species, in spite of wide differences in habitat preferences. Odum (1944) found that the red-backed mouse, *Clethrionomys gapperi maurus*, which occurs only in distinctly wet habitats, drinks from five to thirteen times more water in captivity than other wild mice tested. Vorhies (1945) showed that some desert mammals, such as *Dipodomys*, solve their water problems by conservation of water, effected by physiological and behavioristic adaptations. *Dipodomys* even refused drinking water and succulent food in captivity. Other mammals, *Neotoma*, *Citellus*, and *Lenus*, depended upon utilization of succulent vegetation to maintain their water balance.

The writer wishes to express his most sincere appreciation to Professor S. Charles Kendeigh, under whose guidance the present work was done.

MATERIAL STUDIED

The most thorough attention was given to the northern woodland deer mouse, *Peromyscus leucopus noveboracensis*. The prairie meadow mouse, *Microtus o. ochrogaster*, and the short-tailed shrew, *Blarina b. brevicauda* were also studied. The individual animals used were collected in Champaign County, Illinois except for some of the *Peromyscus* which were from Cheboygan County, Michigan.

The geographical ranges of these species overlap in northcentral United States, but their ecological niches are quite different. *P. l. noveboracensis* inhabits deciduous woods which are dense enough to exclude grassy ground cover. The deer mouse feeds mainly on fruits, nuts and berries, and arthropods, which it collects on the open forest floor. *M. o. ochrogaster* prefers open areas which are sufficiently overgrown by grasses to form a tangled mat near the ground. The meadow mouse feeds on a variety of plant matter which it finds in its runways in the grass. *B. b. brevicauda* is ubiquitous, but its activity is largely in burrows underground or beneath other

¹ Contribution from the Department of Zoology, University of Illinois, Urbana.

natural cover. The shrew feeds largely on insects and other invertebrates, but also takes plant material, particularly small seeds.

Any existing differences of water exchanges correlated with distribution or behavior should be revealed by a study of these three species.

METHODS

The methods are designed to measure directly or indirectly all the means of water exchange between the animals and their experimental environment: the water drunk, water ingested in the food, water of oxidation, water lost by evaporation, and the water lost in the urine and feces. A balance between measured intakes and losses serves as a check on the methods.

GENERAL

The experiments were conducted in two constant temperature rooms in the Vivarium Building, University of Illinois (for description see Shelford, 1929, pp. 404-417). Three temperature ranges were used: 18-19° C, simulating summer temperatures in the deciduous forest; 28° C as the summer temperature of the prairie and 33-34° C as approximating the mean maximum temperature in the prairie, which is near the maximum tolerable to the animals. The relative humidity was kept fairly constant at each temperature by evaporation from large pans of water or by heating water over a hot plate.

Peromyscus and *Microtus* were kept in circular metal cages 3 $\frac{3}{8}$ inches in diameter and 3 $\frac{1}{2}$ inches high, and 6 $\frac{1}{2}$ inches by 4 inches respectively. The sides of the cage were roofing tin and the top was covered with a glass dish. The mice were unable to cling to these surfaces because of their smoothness. The floor of the cage was $\frac{1}{2}$ inch wire mesh. Food and a drinking tube were provided in separate side cubicles. The *Microtus* cage was also provided with a small, well-ventilated, inverted-can shelter. The cages were supported by metal tabs over glass dishes or metal cans containing a half inch of "Finoil." *Blarina* were incompatible with wire mesh and were kept in aquaria. No measurements of urinary and fecal water losses were made for shrews.

The *Peromyscus* were fed only Purina Laboratory Chow; *Microtus* were fed rolled oats, supplemented with sunflower seed between experiments; and *Blarina* were fed raw, ground horse meat, supplemented with fresh mice.

WATER DRUNK

The water bottles were 6 dram shell vials fitted with 8 mm glass drinking-tubes. These bottles were weighed at 24 hour intervals, and the change in weight, minus corrections for any spillage and for evaporation, was taken as a measure of the water drunk during the previous 24 hours. Any spillage was caught in a small dish containing oil placed below the tip of the drinking tube.

FREE WATER IN THE FOOD

The food used was spread out in pans and allowed to come into moisture balance with conditions in the

constant temperature rooms. The percentage water content was determined by periodically drying samples of food in an oven for 48 hours at 100-104° C. The free water in the food eaten was calculated as: (percent water content) \times (air-dry wt. of food eaten/day). Food and water were weighed to an accuracy of 0.01 gram on a triple-beam, agate balance.

URINARY AND FECAL WATER LOSS

The urine and feces were collected free from evaporation under oil in dishes or cans placed under the animal cages. The total weight of these excreta was determined by measuring the 24 hour increase in weight of the collecting container. The urine and feces were then separated from the oil and dried for 48 hours at 100-104° C. The total gain in weight minus the dry weight of excreta was taken as a measure of the water lost in the urine and feces.

To separate the excreta from the oil, most of the oil was decanted, and the remnant: oil, feces and urine, was poured into a small crystallizing dish. This dish was placed under a small-nozzled faucet, and a slow, gentle drip of water was allowed to wash away the oil. Check tests showed that from 0.001 to 0.05 gram of excreta solids was also washed away; this could cause a maximum error of +0.67 percent in measurement of total water losses, but the error was usually much less.

Determination of the fraction of water lost in the feces only was based upon the proportionality existing between the water in the feces and the solid matter in the food eaten (Adolph, 1933). The ratio (R) between the dry weight of feces (f) and the dry weight of food eaten (F) was measured for individual *Peromyscus* and found to be reasonably constant (average 0.335, range 0.329-0.346 at 18° C). i.e. $f=FR$. The percent water content (%W) and percent solid content (%S) of the feces was determined by desiccation of samples (Table 3). If the dry weight of the feces is known, the fecal water (fW) can be calculated as, $fW = \frac{f \% W}{\% S}$, or more simply, if R is known, $fW = \frac{FR \% W}{\% S}$. The dry weight of food eaten (F) is available from daily measurements.

RESPIRATORY EXCHANGES

The water lost by evaporation (insensible water loss, I.W.) and the water of oxidation were calculated from data from direct measurements of respiratory exchanges. An open-circuit chain of apparatus was used to measure these exchanges. The chain was constituted as follows: (1) rotameter for measurement of air flow, (2) drying towers of soda lime and calcium chloride to remove carbon dioxide and moisture from the room air, (3) Unit A, the animal chamber, (4) Unit B, a drying tower of calcium chloride to remove moisture from the chamber air, (5) Unit C, a tower of soda lime for absorption of carbon dioxide, followed by a tower of calcium chloride to absorb the moisture given off by the soda

lime, (6) a vacuum pump. All unit towers were followed by small U-tubes as a check on absorption. Frequent checks of the apparatus showed that pick-up of carbon dioxide and water was 100 percent, within the weighing accuracy used. The animal chamber was a two-quart, wide-mouth mason jar, fitted with a metal cage, drinking tube, food hopper, and temperature recording thermocouple. Oil was placed in the bottom of the jar to prevent evaporation of water from the excreta.

The test animal was confined in the animal chamber for a 24 hour period, except for *Blarina* which were run only six to seven hours. The air flow was adjusted so that the humidity within the chamber would be similar to that experienced by the animal under normal cage conditions. This flow varied from 60 to 250 cc./minute depending upon the temperature. At the beginning and end of each test period all units were weighed on a large-pan, lecture-table balance with an accuracy of 0.01 gram at a load of 2 kilograms. The loss of weight by Unit A, including the animal in the chamber, represented the insensible loss of weight of the animal ($I.L. = I.W. + CO_2 - O_2$). A correction was made for evaporation from the drinking tube. The gain in weight by Unit B measured the insensible water loss (I.W.) of the animal, and the gain of Unit C measured the carbon dioxide produced during the 24 hours. The change in weight of Unit B plus the change in weight of Unit C minus the change in weight of Unit A equaled the weight of oxygen used.

From these data were calculated the total respiratory quotient, the calories of heat produced and the ratio $I.W./I.L.$ The first two were expressed in terms of units per square centimeter of surface area. Surface area was calculated by the formula: $S.A. = Kwt^{2/3}$. Benedict's constant for the white mouse, $K=9$, was used for *Peromyscus*, and $K=7$ was used for *Microtus* and *Blarina* (Pearson 1947).

WATER OF OXIDATION

In the calculation of this exchange, the following factors (Brody, 1945) were used: oxidation within the body of one gram of carbohydrate, fat, and protein produces respectively 0.60, 1.07 and 0.41 cc. of water, and releases 4.10, 9.45 and 4.35 Calories.

From the measurement of respiratory exchanges, the heat production (H.P.) and respiratory quotient (R.Q.) over a 24 hour period were known. The fractions of the heat production due to carbohydrate and fat oxidation were obtained from tables (Brody, 1945:310), and the water resulting from the oxidation of carbohydrate and fat was calculated as follows:

$$\frac{H.P. \times \text{CHO fraction of H.P.} \times 0.60}{4.10} = \text{cc. carbohydrate water of oxidation}$$

$$\frac{H.P. \times \text{fat fraction of H.P.} \times 1.07}{9.45} = \text{cc. fat water of oxidation}$$

This method of calculation results in a certain error since all heat production and water of oxidation are assumed as of carbohydrate or fat origin. The additional accuracy that could be had by measurement of urinary nitrogen and calculation of protein ox-

idation was not deemed worth the necessary extra labor, at least for the objectives of the present study. Calculations indicated that the omission of protein from consideration caused an error of approximately +1.3 percent in the measurement of total intake for *Peromyscus* at 18°C, +0.98 percent at 28°C, and 0.57 percent at 34°C. The degree of the error was less at the higher temperatures because water of oxidation accounted for less of the total turnover then.

INSENSIBLE WATER LOSS

The average daily insensible water loss was calculated using the formula: $I.W. = I.L. \times (I.W./I.L.)$. The total insensible loss (I.L.) for each day was calculated by the formula: $I.L. = (\text{change in body wt. in 24 hours}) + (\text{wt. water drunk} + \text{wt. food eaten}) - (\text{wt. urine} + \text{wt. feces})$. All items of the right half of this equation were measured directly each day. The ratio, $I.W./I.L.$, was determined directly by several respiratory measurements on each individual animal.

The relationship between I.W. and I.L. is not constant, but varies somewhat with the R.Q. and the fraction of heat lost by vaporization of water (Mitchell & Hamilton, 1936). In order to keep these as constant as possible, the animals were maintained on a constant regimen beginning at least one month before the measurements were made. It was estimated that the total water turnover measured by these methods may be in error ± 0.58 percent due to variation of individual measurements of the ratio, $I.W./I.L.$

In the measurement of the total water exchanges, no corrections for errors were attempted. The positive and negative errors were left to balance each other to whatever extent occurred. In practice, for *Peromyscus* and *Microtus*, measured total intake and total loss were in error ± 0.58 percent due to ± 1.5 percent (range 0.4 to 2.7 percent).

MODIFICATIONS FOR BLARINA

Accuracy was more limited for *Blarina*, since the shrews required different housing and food than the mice. The raw horsemeat fed the shrews contained 68 percent water, the evaporation of which complicated the measurement of the free water taken in the food. The shrews were fed at 12-hour intervals and were given only slightly more than would be eaten. At each feeding an extra measure of meat was placed out to act as an evaporation standard; 25.5 percent of the water content evaporated in 12 hours. Observation showed that the shrews ate the meat at a relatively continuous and constant rate. Therefore the amount of water evaporating from the food per unit time would decrease as the food was eaten. Of the total amount that would evaporate if the food were not eaten, 87.2 percent is actually ingested and only 12.8 percent evaporates.

Water of oxidation was calculated from the weight of meat eaten, assuming a 16 percent fat and 16 percent protein content, and also assuming that only 92 percent of the protein and 95 percent of the fat

is actually digested, the remainder being lost in the feces (Brody, 1945). Then, gm. food eaten $\times .16 \times .95 \times 1.07 =$ cc. fat water of oxidation; gm. food eaten $\times .16 \times .92 \times .60 =$ cc. protein water of oxidation.

The I.W. and I.L. were measured directly during respiratory exchange measurements which were run as for mice except that they lasted only six to seven hours and no food was allowed during the measurements.

Since urine and fecal water loss could not be measured, the measured total intake was used as the level at which water equilibrium occurred.

PROCEDURE

Because of the labor involved in the methods, the size of the experimental group was limited to five animals of each species, three males and two females. These individuals were carried through the entire series of experiments at the different temperatures. The high temperature of the last experiments at 33-

34°C caused some fatalities, reducing the *Peromyscus* group to four animals and the *Microtus* to three.

The experiments on each species were conducted in several successive steps as follows: (1) one month or more of acclimation to the conditions of temperature and humidity and to the feeding, watering and handling schedule, (2) one 24 hour measurement of respiratory exchanges for each animal, (3) measurement of all paths of water exchange for 14 to 24 days, (4) one or two 24 hour measurements of respiratory exchanges, (5) measurement of the specific gravity of the urine and the water content of the feces. *Peromyscus* was studied at 18°, 28° and 34° C, *Microtus* at 28° and 33° C, and *Blarina* at 19° C only.

An additional group of five *Peromyscus* was used at 28° C in order to study the effects of various degrees of restriction of water intake. Particularly, complete water exchanges were measured over a 15 day period when the mice were receiving an average

TABLE 1. Summary of the data for the water exchanges of *Peromyscus*, *Microtus*, and *Blarina*. Data are in terms of cc./animal/day; each datum is an average figure for all animals in the experimental group. Percentages refer to percent of total turnover; each percentage is an average of percentages calculated for individual animals in the group.

Animal	Conditions	Weight in gms.	Water drunk		Water in Food		Water of Oxidation		Urine-Fecal Water Loss		Insensible Water Loss		Total Water Turnover cc.
			cc.	%	cc.	%	cc.	%	cc.	%	cc.	%	
A. <i>Peromyscus</i> ..	17.8° C 62.5% R.H.	20.66	5.36	72.3	0.43	6.0	1.60	21.7	4.80	64.9	2.60	35.1	7.40 ± .10
B. <i>Peromyscus</i> ..	28.1° C 50.5% R.H.	20.61	10.18	85.0	0.22	2.9	0.93	12.1	7.38	60.2	3.41	39.8	11.18 ± .27
C. <i>Peromyscus</i> ..	34.2° C 43.5% R.H.	20.40	13.38	93.0	0.19	1.4	0.78	5.6	7.00	52.2	6.88	47.8	14.11 ± .23
D. <i>Microtus</i>	28.1° C 50.5% R.H.	42.64	15.80	89.2	0.26	1.8	1.38	9.0	14.42	80.6	2.92	19.4	17.40 ± .08
E. <i>Microtus</i>	33.2° C 44.5% R.H.	38.62	16.59	92.3	0.16	0.9	1.09	6.8	13.24	74.4	4.42	25.6	17.75 ± .16
F. <i>Blarina</i>	18.7° C 54.5% R.H.	25.76	5.75	37.4	6.79	45.5	2.55	17.1	15.09
G. * <i>Peromyscus</i> ..	27.6° C normal	23.18	9.08	83.1	0.26	3.1	1.05	13.8	6.80	60.0	3.59	40.0	10.38
H. * <i>Peromyscus</i> ..	27.6° C restricted	20.05	1.71	63.4	0.14	5.2	0.82	31.4	1.32	51.2	1.27	48.8	2.63 ± .07

*Group of mice used for water-intake restriction experiments.

TABLE 2. Summary of data for the water exchanges of *Peromyscus*, *Microtus* and *Blarina*. Data are in terms of cc./cm.² surface area/day, and each datum is an average figure for all animals in the group; s indicates one standard deviation for the group.

Animal	Temp. °C	Surface Area cm. ²	Water Drunk		Water in Food		Water of Oxidation		Urine-Fecal Water Loss		Insensible Water Loss		Total Water Turnover	
			cc.	s	cc.	s	cc.	s	cc.	s	cc.	s	cc.	s
A. <i>Peromyscus</i> ..	17.8° C	67.69	.079	.009	.0063	.0002	.023	.0022	.071	.009	.039	.006	.110	.011
B. <i>Peromyscus</i> ..	28.1° C	67.99	.145	.100	.0033	.0003	.014	.0004	.104	.089	.070	.018	.158	.104
C. <i>Peromyscus</i> ..	34.2° C	67.12	.199	.065	.0028	.0002	.011	.0020	.104	.024	.102	.048	.210	.065
D. <i>Microtus</i>	28.1° C	86.41	.181	.068	.0030	.0002	.016	.0010	.164	.068	.034	.004	.199	.067
E. <i>Microtus</i>	33.2° C	82.81	.198	.064	.0020	.0006	.013	.0013	.158	.055	.053	.016	.211	.064
F. <i>Blarina</i>	18.7° C	60.77	.096	.039	.112	.012	.042	.004250	.055
G. * <i>Peromyscus</i> ..	27.6° C	72.96	.1260035014095048448
H. * <i>Peromyscus</i> ..	27.6° C	66.31	.025400210123019701900394

*Group of mice used for water-intake restriction experiments.

of only 26 percent of the amount of water they would drink *ad libitum*.

RESULTS

Data for water exchange measurements are summarized in Tables 1 and 2. In order to make comparisons between the three species, the data were originally reduced to three reference bases: surface area; weight 0.70 , which seems to fit many biological functions (Brody 1945); and weight 1.0 . Examination showed that none of these bases was uniformly good for all three species, for one species at different temperatures, or even for all paths of exchange of one species at one temperature. Probably no such base should be expected. Surface area was the most consistently good base for *Blarina* and *Peromyscus*, while weight 1.0 was best for *Microtus*.

At a temperature of 19°C , *Blarina* had a level of water equilibrium more than double that of *Peromyscus*. The shrew got almost half of its water intake in the food eaten, but still drank slightly more than *Peromyscus*, showing that a need to drink may exist even if considerable water is gotten from very moist food. *Blarina* also derived more water from oxidation, because of a greater food intake and higher fat content of that food.

At 28°C the individual *Microtus* had an average total turnover 56 percent greater than *Peromyscus*. But, on the basis of rate of exchange per cm^2 of surface area, there was no significant difference between these species.

WATER DRUNK

For mice on a dry diet, water drinking is the most important path of intake. With increase of temperature, the water drunk becomes an increasingly larger part of the total intake.

As indicated by the standard deviations in Table 2, there was considerable variation among individuals of the same species. Variation was least for *Peromyscus* at 18°C and for *Microtus* at 28°C ; these temperatures are more normal to the natural environment of these species than the other temperatures used. Those water exchanges which are more or less dependent upon metabolism, i.e. water of oxidation, water in food, and insensible water loss, were much more constant than the amount of water drunk, which may vary with individual differences in drinking habits, behavior, and activity. *Peromyscus* at 28°C showed very great individual variation in the amount of water drunk, ranging from an average of 3.19 to 19.11 cc./day. Two mice in the group met the unnatural conditions of this temperature by reducing their losses, and maintained a level of drinking (3.19, 3.59 cc./day) actually about 1.4 cc. below that at 18°C . A third mouse increased its drinking only .7 cc./day, while the other two mice more than tripled their drinking. The mice were consistent, however, in the amount of water drunk, every day drinking either the larger or smaller amount. A similar condition is reported for *Dipodomys* by Howell & Gersh (1935).

It seems certain that the mice drinking 18.6 and

19.1 cc./day were drinking far beyond their basic requirements, excesses of water intake being returned in the urine. However, the mice were responding to some definite urge to drink. When such individuals were limited in their intake, they showed definite signs of thirst; when returned to *ad libitum* intake, they quickly reestablished their former high level of drinking.

Some data indicated that mice having the shelter of a nest drink less and are individually less variable. An additional group of five *Peromyscus*, which were allowed cotton nesting material in a larger cage, drank 4.52 (2.56-7.05) cc./day at 33.5°C . Dice (1922) allowed nesting material and found that *Peromyscus* drank only 1.64 (1.45-1.79) cc./day at 28°C , while *Microtus* drank 4.35 cc. For various species of deer mice, allowed nests, Ross (1930) reported averages of 2.16 to 4.08 cc. drunk per day at $22-23^{\circ}\text{C}$. The greater humidity of the air within a nest would reduce the evaporative losses from skin and lung surfaces, and would also reduce the sensations of thirst due to drying of the mucous membranes in the oral cavity and pharynx. Cannon (1918), Bellows (1939), and others have shown the latter to be a factor in thirst and increased water intake.

FREE WATER IN THE FOOD, WATER OF OXIDATION

The intake along these paths becomes less as the food intake is reduced at higher temperatures. When water is allowed *ad libitum*, these intakes are relatively insignificant, but for *Peromyscus* during the restricted drinking experiments, water of oxidation was an important 31 percent of the total intake. In their natural habitats, *Peromyscus* and *Microtus* undoubtedly get more water in their food, and this is probably their major means of intake. Babcock (1912), on the basis of his pioneering work on metabolic water, concluded that the water derived from intracellular oxidation of organic material would probably be sufficient for all animal needs if it were not for the water required for the excretion of waste products of protein oxidation. Dice (1922) showed that *Microtus* can survive quite well when fed only green grass and given no drinking water.

URINARY AND FECAL WATER LOSS

The urinary loss is the most variable path of exchange. A certain amount of water is required to keep urine solids in solution, but beyond this the renal output depends upon the amount of water liberated by the tissues. Any changes in other paths of intake or loss are quickly reflected by changes in the urinary output. Figure 1 shows that for *Peromyscus* the rate of urine-fecal water loss was greater at 28°C than at 18°C , reflecting the increased intake. At 34°C the intake was still larger, but since evaporative losses increased at a proportionally greater rate, the additional intake was eliminated by vaporization rather than by an increase in the renal loss, which remained at its 28°C level.

When it is necessary to conserve water, the greatest saving can be effected by reduction of urine vol-

ume. *Peromyscus* on a water-restriction regimen at 27.6° C reduced their average urine-fecal water loss to 19 percent of normal, a reduction of 5.48 cc.; the average insensible water loss was reduced to 35 percent of normal, a saving of only 2.32 cc.

The specific gravity of the urine was determined by the benzene-chloroform method; samples were taken over 24 hour periods to eliminate diurnal variation. Data for these measurements, and for fecal water content are given in Table 3.

TABLE 3. Data for the specific gravity of the urine and water content of the feces of *Peromyscus* and *Microtus*.

	Specific gravity of urine	Water content of feces, percent	WATER LOST IN FECES	
			percent total loss	cc./day/animal
<i>Peromyscus</i>				
18°C....	1.062 (1.033-1.087)	54.4	23.9	1.77
28°C....	1.040 (1.007-1.058)	45.2	5.4	0.59
34°C....	46.5	4.0	0.55
27.6°C. R.	1.076 (1.063-1.097)	41.6	14.7	0.38
<i>Microtus</i>				
28°C....	1.021 (1.012-1.036)	50.0		
33°C....			

The specific gravity of the urine varied inversely with the urine volume. The value, sp.gr. 1.097, indicates that deer mice can produce a very concentrated urine. The water content of the feces of these mice was considerably less than the figure of 70 percent generally used for white mice (Bing & Mendel, 1931). The data indicate that mice on restriction (27.6° C R) may possibly conserve some water by reducing the percent water content of the feces.

THE INSENSIBLE LOSS OF WATER

As shown in Figure 1, the rate of insensible water loss increases with the temperature. Limited data indicate that *Blarina* has the greatest rate of loss of the species studied, and this rate increased rapidly even at low temperatures (350 percent between 18° and 28° C). For *Peromyscus* the average rate of vaporization increased only 28 percent between 18° and 28° C, but then increased 104 percent between 28° and 34° C. In the matter of evaporative losses, *Microtus* is definitely different from *Peromyscus*. Although the *Microtus* had 1.25 times more surface area, their average evaporative loss was 14 percent less than that of *Peromyscus* at 28°. The average insensible water loss of *Microtus* increased only 51 percent between 28° and 33° C, so that at the latter temperature *Microtus* lost 36 percent less water by evaporation than did *Peromyscus*. On a surface area basis, the rate of loss in *Microtus* was also significantly lower.

Figure 2 shows further the relation of vaporization to temperature. The "basal" data are for respiratory measurements made on *Peromyscus* in a post-absorptive state. The mice were confined in a wire cage only slightly larger than their body in

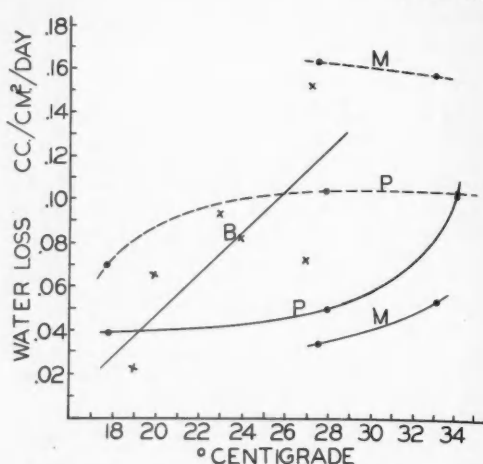


FIG. 1. The relation of urine-fecal water loss, and insensible water loss to temperature. Solid-line curves are data for the insensible water loss of *Peromyscus* (P), *Microtus* (M) and *Blarina* (B). Broken-line curves are data for urine-fecal water loss.

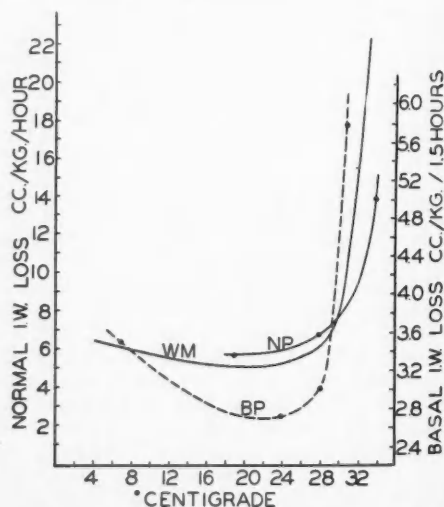


FIG. 2. Relation of insensible water loss to temperature. NP=data for normal *Peromyscus*, BP=data for "basal" *Peromyscus*, WM=data of Chevillard (1935) for the white mouse.

order to limit activity. The measurement periods were divided into 1½ hour intervals, and data for intervals with marked activity were not used. The data of Chevillard (1935) for the white mouse are included for comparison. All curves show a sharp upward turn at 28° to 30° C, indicating the beginning of some physiological mechanism to increase vaporization in the interest of temperature regulation.

This increase cannot be accounted for in physical terms since the skin temperature approaches a rela-

tively constant level at an air temperature of 30° C, and increases only about 1.5° C between air temperatures of 30° to 40° C (Herrington 1940). For nonsweating species, which include mice, the physiological mechanism is generally indicated to be an enormous increase in breathing rate. Such has been reported for cattle, sheep, swine and the dog (Brody, 1945) but not for smaller mammals. The breathing rates of "basal" *Peromyscus*, taken simultaneously with the data of Figure 2, are:

Air temp. °C	Breathing rate/minute
7	236
24	140
28	138
32	141

Data for other *Peromyscus* when normally active are:

Air temp. °C	Breathing rate/minute
15	199 (169-230)
26	169 (144-204)
35	194 (174-206)
27.6 R	175 (140-212)

There was a higher rate of respiration at lower temperatures, referable to the higher metabolism then, but there was no significant increase in the rate of respiration as the temperature increased above the zone of thermal neutrality (assumed at 28° C). It is possible that there was an increase in the volume of air breathed, which would increase the insensible water loss. *Peromyscus* on a restricted water intake (27.6° C R) did not reduce their rate of breathing although their metabolism fell to 75 percent of normal. Such a reduction in breathing has been reported for *Dipodomys* (Howell & Gersh 1935). Neither did the mice try to cool their skin at high temperatures by spreading saliva on their fur, beyond the normal amount, as reported for white mice by Herrington (1940).

The primary role of insensible water loss is for heat regulation, particularly at high temperatures when heat loss by radiation, conduction and convection is greatly reduced. Figure 3 shows the fraction of the total heat loss occurring by vaporization at different temperatures, as calculated from respiratory exchange data. *Microtus* was significantly less efficient than *Peromyscus* in losing heat in this manner. Data for the white rat (Swift & Forbes 1939) are similar to those for *Peromyscus* except that the vaporization heat loss increased more slowly at high temperatures.

Figure 4 shows that for *Peromyscus* at 28° C there was a direct relation between the amount drunk and the amount vaporized. Limited data for *Microtus* showed no such relation.

Experiments on water restriction show that when *Peromyscus* needs to conserve water, the insensible water loss can be reduced to the least amount and becomes the greatest path of loss, the critical point in the water economy of the animal.

Microtus lives in the habitat most susceptible to desiccation. During drought, when water conser-

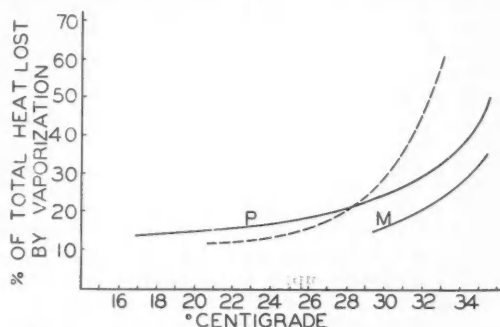


FIG. 3. Relation of percent of total heat loss occurring by vaporization to temperature. Solid-line curves are data for *Peromyscus* (P) and *Microtus* (M); broken-line curve is data of Chevillard (1935) for the white mouse.

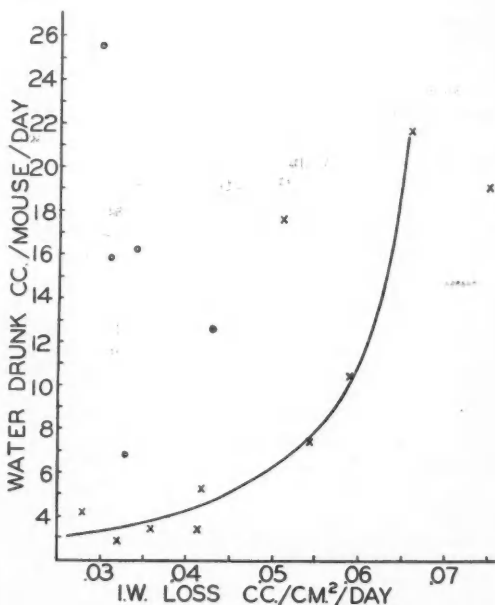


FIG. 4. Relation of insensible water loss to amount of water drunk. Curve and x's are data for *Peromyscus*; o's are data for *Microtus*.

vation is necessary, *Microtus* would have an advantage over *Peromyscus* in that its evaporative loss is initially lower. However, if the drought were accompanied by high air temperatures, *Microtus* would be at a disadvantage. Its lower evaporative loss would mean less heat lost by vaporization and thus less efficient regulation of body temperature than *Peromyscus*. Heat losses might be so inadequate as to allow a fatal rise in body temperature, which may account for the observed discomfort of *Microtus* at air temperatures of 35° C or over. *Microtus* observed at these temperatures were always spread out flat on the floor of the cage, possibly to increase their evaporative surface area. *Peromyscus* showed no out-

ward signs of discomfort at 37° C. Two *Microtus* died when the temperature in the respiratory-apparatus animal chamber remained at 36° C for about two hours. Dice (1922) also noted an intolerance of *Microtus* for temperatures over 36° C.

RESPONSE TO RESTRICTION OF DRINKING WATER SUPPLY

Tables 1 and 2, lines (G) give the data for normal water exchanges of the five *Peromyscus* used in the restriction experiments. The data compare favorably with those for the other group of *Peromyscus*, (B).

When the water supply was limited to 75 percent of what would normally be drunk ad libitum, there was a varied response. The weight of two mice did not change; two other mice lost two to three grams, which they regained after several days on the restricted regimen; one mouse consistently lost weight, indicating that 75 percent was below the amount required for its normal maintenance. For the group, the minimum intake by drinking necessary for normal maintenance, as indicated by body weight maintenance, averaged 2.58 (range 1.12-4.10) cc./day, and was an average of only 39.4 percent of their normal drinking intake. In four cases the food intake fell to 77 percent of normal when drinking was restricted, and daily fluctuations in body weight were definitely correlated with fluctuations in food intake. It is probable that water restriction affects body weight largely by curtailment of the food intake. One mouse lost weight even though it kept up a normal food intake, indicating the loss was due to water deficiency per se.

When the mice were returned to ad libitum water drinking, lost body weight was recovered largely within the first 24 hours, and the mice returned finally to an average of 97 (84-110) percent of their previous weight. During recovery the water drinking fluctuated widely, but after six to eight days was approximately at its former level. Food was eaten in excess of normal for the first six days. During restriction there was a gross "deficit" between the forced low level of water and food intake and the amount that would normally be taken in ad libitum. The intake in excess of normal during recovery represented only 50 percent of the gross "deficit" in food intake and 17 percent of the gross water deficit. Thus the adaption to the gross "deficit" was more by reduction of water losses and more efficient use of food during restriction, than by excess intake after restriction. The actual deficit at the end of restriction was greater for food than for water. The white rat reacts similarly to restriction, but for the dog, recovery intake largely replaces the gross deficit, while the rabbit is intermediate in reaction (Adolph 1947).

A sudden, one-day deprivation of water was accompanied by a drop in food intake to 37 percent of normal and a loss of 14.6 percent of the initial body weight. This is significant to the extent that normal body weight fluctuated only an average of 0.3 percent per day, but 14.6 percent probably represents no more than the weight of the alimentary tract con-

tents, plus a small tissue loss. Chevillard (1935) found that the weight of the white mouse may vary 6 to 12 percent during one day due to alimationation.

A one-day deprivation of food caused a loss of 12.9 percent of the body weight.

Tables 1 and 2 (H) give the data for water exchanges during severe water restriction. This experiment lasted 15 days, during which time the mice were allowed to drink only 1.71 (1.08-2.31) cc./day, or an average of only 26 (8-42) percent of their ad libitum drinking intake. The amount, 1.71 cc./day, is 34 percent less than the average amount the mice needed for normal maintenance, but happens to be almost the same as the normal intake found for *Peromyscus* at 28° C by Dice (1922). When these data were examined on a day-to-day basis, it was found that water losses exceeded intake only for the first two or three days, creating an initial negative water balance. By that time the mice had reduced their losses and were able to maintain intake slightly in excess of loss so that the initial deficit was gradually made up in about 15 days. Figure 5 shows this response for two mice. The urine-fecal water loss was reduced most sharply, so that the reduction necessary to regain water equilibrium was effected by the second day. The insensible water loss declined more slowly, the necessary level being reached by the fourth to seventh day.

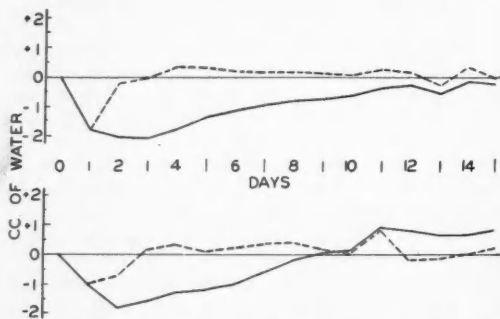


FIG. 5. Water balance of two individual *Peromyscus* when restricted to 26 percent of the amount of water normally drunk ad libitum. Broken lines represent daily water balance; solid lines represent cumulative water balance. Restriction was begun at zero days.

A comparison was made between the data for respiratory exchange measurements made just before the 15 day restriction period, and those made at the end of the period. This showed that during restriction the respiratory quotient changed only slightly, from 0.935 to 0.922, while the rate of metabolism dropped 25 percent from 0.102 Cal. to 0.076 Cal./cm.²/day. The rate of insensible water loss decreased from 0.019 to 0.009 cc./cm.²/day. Related to this, the amount of heat lost by vaporization dropped to 77 percent of normal, and the ratio, I.W./I.L., necessary in calculating the average daily I.W., shifted from 0.688 to 0.613.

During the 15 day period of restriction, the intakes and losses of the mice were measured to an equi-

librium in error only 2.4 percent. This indicates that the described methods can be applied successfully to an abnormal situation such as exists under restriction, if the measurements are made over a sufficiently long time, and if respiratory exchange measurements are made frequently in order to detect any changes in the ratio, I.W./I.L.

At the beginning of the restriction period, the mice weighed an average of 23.4 grams. During the first 15 days their weights dropped to an average low of 17.9 grams. When they were continued on a restricted drinking intake averaging 1.71 cc./day, the mice slowly gained to an average weight of 18.6 grams at 61 days and 19.4 grams at 129 days. This shows that the individual mouse is able to survive a severe water restriction for some time.

When the mice were then allowed only 0.60 cc. drinking water per day, food intake dropped to 41 percent of normal and body weight was lost rapidly. Three mice died after six to nine days of this restriction, after having lost 36 to 53 percent of their initial weight. The other two mice, having lost 31.6 and 44.8 percent of their initial weight, were in very poor condition, barely able to stand. When they were returned to an unlimited water supply, they gained 5 grams the first day and 9 grams by the end of the third day. One of the mice was accidentally lost, but the other remained in good health for the next two weeks, after which the experiment was ended. At the time of death from water restriction, the mice had an average body water content of 66.6 percent, as compared with 65.5 percent for normal mice. This indicates that the mice died from starvation or other causes, rather than from dehydration.

DISCUSSION

The water turnover of a small mammal depends upon: (1) the availability of water in its environment, (2) environmental factors determining loss of water, (3) various physiological features of the animal.

The availability of water in an environment is very difficult to measure. Because of limited home range, few small mammals encounter surface water, so that their main intakes must be as water in the food, and the drinking of dew and rainwater. Just how much water small mammals can get in this latter fashion is not known.

In feeding on invertebrates, *Blarina* gets a food of high water content, 60 to 95 percent. The forest fruits, nuts, and berries eaten by *Peromyscus* would provide somewhat less water: acorns 38-47 percent water, hickory and walnuts 2 to 3 percent, berries and fruits 75-85 percent (Waino & Forbes 1941). The diet of *Microtus* would provide considerable water when the vegetation is green, but this diet is exposed to the most desiccation, particularly during drought. Judging from food habits, it is probable that *Blarina* has the greatest available water supply and *Microtus* the least, particularly for critical times of the year.

In ingesting the same caloric content, *Blarina* would get more water than the other two species, and

thus have a larger water turnover. Experiments showed that *Blarina* does have the highest water intake, drinking a large amount of water even though eating very moist food. *Peromyscus* and *Microtus* had similar rates of turnover per cm.² of surface area, though the individual deer mouse drank less.

Estimation of the evaporative forces in different habitats, and of evaporative losses of small mammals living in these habitats, is hazardous because the numerous factors involved in evaporation are often difficult to measure, and further, there are few data for the conditions of temperature, humidity and air movement actually encountered by small mammals in their runways, burrows, nests and on the ground surface.

In the present work a need was felt for some sort of analysis of the evaporative forces within the habitats of the animals studied. This analysis was limited to a study of $(E_0 - e_1)$, the difference between the vapor pressure of the evaporating surface and that of the overlying air. E_0 was taken as the vapor pressure of saturated air at skin temperature; skin temperature was calculated as $T_{\text{skin}} = 16.6 + (0.70 \times T_{\text{air}})$, from the work of Herrington (1940) on the guinea pig. The vapor pressure of the air was calculated from the limited data of Weese (1924) and Johnson (1926) for the air temperature and relative humidity on the grassland floor, the forest floor, and within the forest soil (data for Trelease Woods and adjacent grassland, Champaign County, Illinois).

This analysis indicated that for the limited data, evaporation from a small mammal would be greatest in the prairie and least within the forest soil in a ratio of 75:66:47::grassland floor:forest floor:forest soil. The validity of this relationship certainly needs further study.

Therefore, *Blarina* is subjected to less evaporation because of the physical features of its subterranean habitat than either *Peromyscus* or *Microtus*. When *Blarina* was experimentally compared under the same conditions with these other animals, it lost more water by evaporation than either. This can be due to: (1) its greater water intake, since there is some direct relation between intake and evaporation (at least for *Peromyscus*), (2) physiological differences, and/or (3) an inability to conserve evaporative losses because of lack of demand for this physiological response in its natural environment. *Microtus*, which meets the most severe evaporative conditions, had the lowest rate of evaporative loss under experimental conditions, and showed an ability to conserve its losses better under the stress of high temperature, possibly a physiological feature developed in response to the demands of its environment.

Peromyscus inhabits an environment of intermediate evaporative forces, but experimentally it showed an ability to survive very severe water restriction, such as might be met during a prairie drought. However, survival of the individual does not imply survival of the race, the continued existence of which depends upon successful reproduction in the face of environmental resistance. Subjection of a popula-

tion to a habitat with foreign conditions of water availability and evaporation might affect some critical point such as the water requirements of the lactating female, and reduce the biotic potential to such a point that the population would gradually die out.

Some correlation may exist between the availability of water and the evaporative forces within an environment and the habitation of that environment by a particular animal, such habitation depending upon at least equality between the water turnover required by the animal and that allowed by the environment. *Blarina* may be unable to leave its subterranean habits partly because the evaporative losses caused by the forest or prairie floor may be too great for its water turnover. Likewise, *Peromyscus leucopus* may be unable successfully to live in open grassland.

However, at present there is insufficient evidence to say that water requirements determine the habitat distribution of the animals studied, or even to state the relative importance of water requirements in this distribution. In past history, when small mammals had more plastic and more generalized habitat preferences, water requirements may have been a deciding factor in their distribution. Each species may have gradually settled into an environment which was satisfactory for its water requirements yet unsatisfactory for other forms, thus reducing interspecific competition. Present mammals, however, are structurally, physiologically, and psychologically adjusted in many ways to their environment. So, the removal of a present limiting factor, such as environmental water supply, would not necessarily allow the limited animal to extend its distribution into a habitat otherwise foreign to it.

SUMMARY AND CONCLUSIONS

Methods were developed by which all paths of water exchange between small mammals and their environment were measured.

A general correlation exists between the rate of evaporation and availability of water within a species' habitat and the level of its water exchanges. The subterranean *Blarina b. brevicauda* had the largest water turnover; at 19° C it was twice that of the nocturnal, forest-inhabiting *Peromyscus leucopus noveboracensis*. *Blarina* drank considerable water even though eating food of high water content. The grassland-inhabiting *Microtus o. ochrogaster* had a rate of turnover similar to that of *Peromyscus*, but showed a significantly lower loss through evaporation, possibly an adaptation to its drier habitat.

Evaporation of water from the lung and skin surfaces appeared physiologically to be the most important means of water loss, because of its effect on the water balance and on temperature regulation. *Blarina* had a rate of loss which increased rapidly even at low temperatures (350 percent between 18° and 28° C). Possibly this alone would prevent *Blarina* from permanently inhabiting a surface habitat. The rate of evaporation of *Peromyscus* increased only 28 percent between 18° and 28° C, but in-

creased 104 percent between 28° and 34° C. The rate of *Microtus* vaporization increased only 56 percent between 28° and 33° C, and at the latter temperature was only half that of *Peromyscus*.

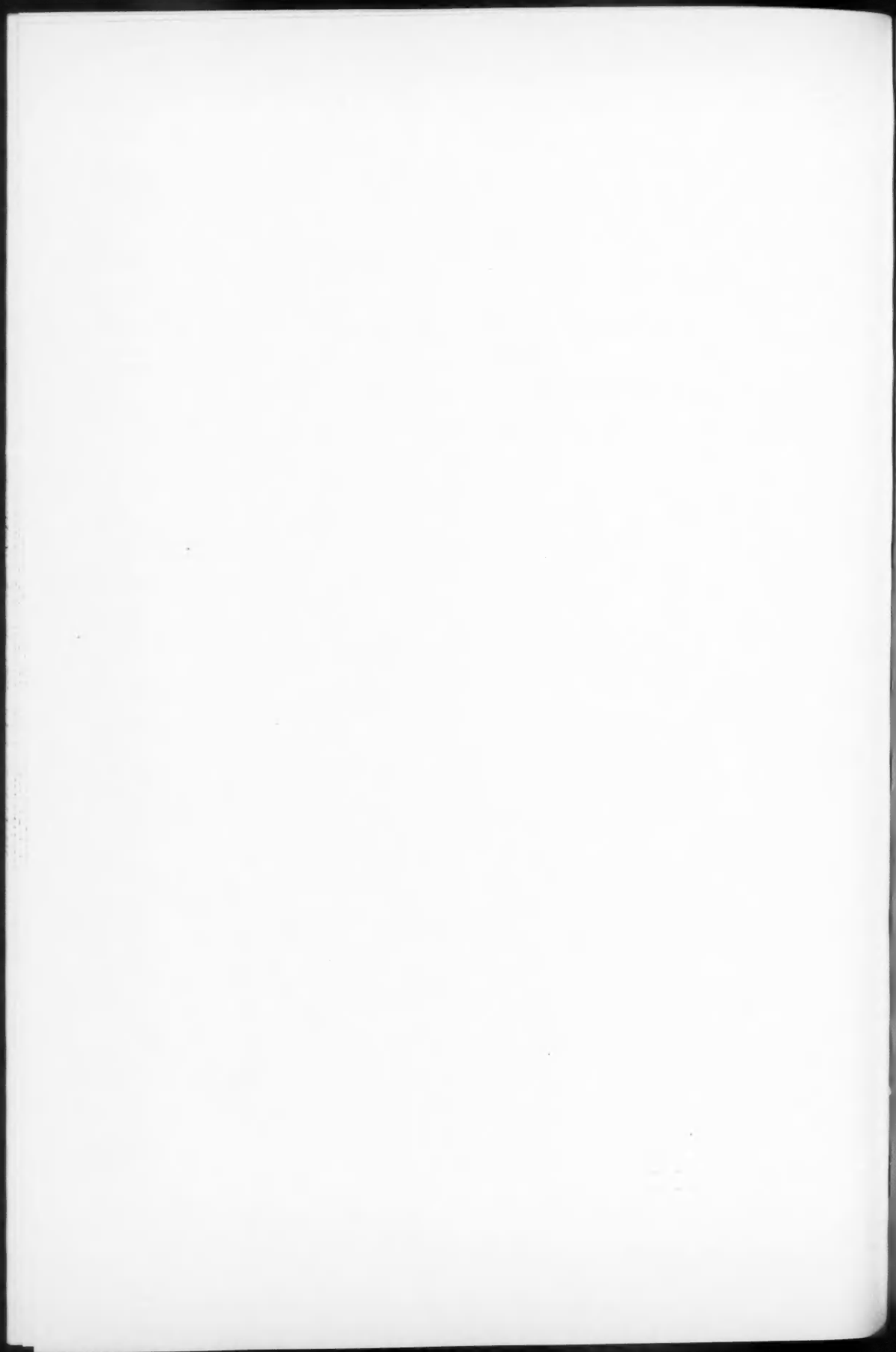
Above 28-30° C the rate of vaporization of *Peromyscus* increased for temperature regulation by some physiological means, other than increased breathing rate. At 34° C *Peromyscus* lost 38 percent of its heat by vaporization, while *Microtus* lost only 27 percent. Probably because of this poorer temperature regulation, *Microtus* showed evident physical discomfort at temperatures of 35° C or over, while *Peromyscus* did not. For *Peromyscus* at 28° C there was a direct relation between the amount of water drunk and the amount vaporized.

For *Peromyscus*, when water drinking was restricted, most water conservation was effected by a reduction in urine volume. Evaporation was reduced less and became the greatest path of loss. *Peromyscus* required an average of 39 percent of the amount it normally drank *ad libitum* in order to maintain normal body weight. Restriction to less than this curtailed food intake sufficiently to cause weight loss. Although showing definite thirst, *Peromyscus* survived four months on only 26 percent of the *ad libitum* drinking intake. Restriction to this level was accompanied by an initial negative water balance for two or three days, but by then a slight positive balance was developed which restored water equilibrium in about 12 days. During this time water of oxidation formed an important 31 percent of the total water intake. Individual mice recovered from more severe restriction after losing 32-45 percent of their initial weight. Mice dying from the results of water restriction had a normal body water content of 66 percent.

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VEGETATION AND HABITATS IN A SOUTHWESTERN VOLCANIC AREA

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	227	LAVA SINK-HOLE PONDS	243
CLIMATE	229	Rock-crust Algal Community.....	245
LAVA FLOW SURFACE COMMUNITIES.....	230	Ooze Community.....	245
The Douglas Fir Belt.....	230	Submerged Aquatics.....	247
The Ponderosa Pine Belt.....	232	Reed Marsh Stage.....	247
The Apache-Plume Belt.....	236	ICE CAVES.....	247
SUBSTRATES AND PLANT DISTRIBUTION.....	238	Zonation in Ice Cave Entrances.....	249
Cinder Benches.....	240	OTHER SHELTERED TERRESTRIAL HABITATS.....	251
Cinder Cones.....	241	SUMMARY	252
		LITERATURE CITED	253

INTRODUCTION

One of the most extensive and least known areas of recent volcanism in this country lies east of the continental divide in west-central New Mexico. The various flows occur largely in Valencia and McKinley counties. Extending northeast-southwest for more than a hundred miles, the area's length is nearly equally bisected by the Rio San Jose at Grants. Most of the extrusive material of the general region is considered late Tertiary (Dutton 1886; Darton 1928). Hooper (1941) has published a brief general description of the physiography and geology in and about the lava area. He also gave more detailed descriptions of his various stations for collecting mammals.

In the present study emphasis was centered on an area of 220 square miles southwest to east of Grants, shown within the solid line and the northeast dashed boundary of Figure 1. The junction of the meridian of 108° W. and the parallel of 35° N. falls not far north of the main body of this lava flow. The map was prepared from airphoto mosaic sheets on which the distinct black shade indicates largely the Quaternary, probably mostly Recent, lava. This material is

¹ The writer is grateful for the help of many. The Purdue Research Foundation supported a large portion of the work. The Governor and tribal council of the Acoma Pueblo, David Candelaria, and William Porter gave access to certain lands. Specialists furnishing plant identifications were: Mr. E. B. Bartram, mosses; Fay K. Daily, Characeae; Dr. C. W. Dodge, lichens; Dr. Francis Drouet, algae; Dr. A. W. Evans, hepatics; Mr. C. V. Morton and others of the U. S. National Herbarium, many of the herbs; and Dr. G. W. Prescott, algae. Prof. E. L. Martin ran chemical analyses of water, Dr. Helmut Kohnke advised on soils, Mrs. Lela McCord supplied her IX-XI Ranch meteorological records, and the Albuquerque office of the U. S. Weather Bureau loaned an instrument shelter and rain gage. Thanks go to the officials and staff of the Navajo Fluorspar Mine, particularly Mr. G. A. Warner, Mr. J. H. Mallory, and Mr. and Mrs. M. Houston, for making available a field laboratory and living quarters and for many kindnesses.

rough and unweathered, showing very little soil accumulation; the youngest portion is believed to have flowed very recently, possibly within historic times. The area near Grants outlined by a dashed boundary is distinctly older than the narrow tongue adjacent to it farther east. These flows partly overran much weathered lava of Tertiary age, which appears light on airphotos because of its soil mantle of windblown silt, or of pumice from nearby cones. The large flat plain south of the continental divide where volcanic peaks dot the map, is of Tertiary lava covered largely with aeolian deposits. In the broad body of the flow appears a large, roughly triangular area of the same nature, which the recent flows failed to cover. The general highway map of Valencia County prepared by the New Mexico Highway Department (1938) omits many of these features.

The dark gray or black, sometimes reddish, younger basalt forms a conspicuous scenic feature popularly called the "malpais." A number of color photographs of this lava bed's scenery were published by Clark (1946) in a popular magazine article. This malpais has been called the "Grants Lava Bed," the "McCarty's Lava," and the "Agua Fria Malpais" by different writers. It is general practice to use the name of the nearest town, Grants, for the 220 square mile deposit of largely Quaternary lava, instead of restricting the name, as Hooper did, to a small portion of the flow nearest Grants.

This recent lava bed stretches 30 miles in length and ten miles in maximum width. Its altitude ranges from 8,308 feet at the summit of Flagpole Cone, the crater of which (Fig. 2) supplied much of the magma, to 6,200 feet at the northeast terminus near McCarty's village. The latter part of the bed has been described by Nichols (1939a, 1939b) in publications dealing with flow mechanics. Within the higher part of the Quaternary bed are at least nine lava or lava-and-cinder cones, and southwest of it an inaccessible plateau region of probably Tertiary lavas extends for miles, with very many volcanic

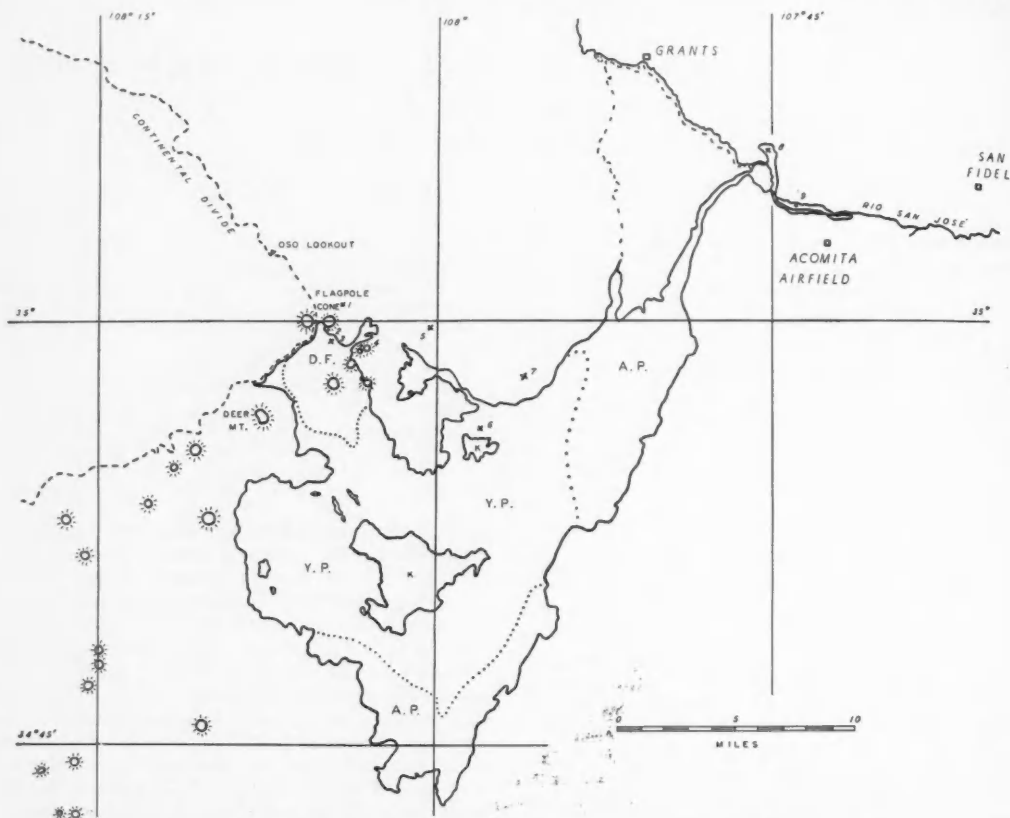


FIG. 1. Map of the Grants Lava Bed and vicinity, Valencia County, N. M. Numbered localities are: (1) Cinder Hill, (2) Ice Cave Resort, (3) Douglas fir lava station, (4) Marchantia ice cave, (5) Navajo Fluorspar Mine, (6) Ponderosa pine lava station, (7) IX-XI Ranch weather station, (8) Apache-plume lava station, (9) Asplenium pit, nearby ponds and caves near Anzac village. D. F., Douglas fir belt; Y. P., ponderosa pine belt; A. P., Apache-plume belt; K, kipouka (island) of ancient lava or non-lava bedrock. The dashed border of the northeast lobe indicates lavas mostly older than Recent, or soil-covered.



FIG. 2 The breached south side of Flagpole Cone. The highest Douglas firs on the lava bed show in the middle distance.

cones. Of all these peaks, including many of material size, only two appear on any previously published map.

The early human history of this vicinity may be briefly recalled. Varied types of Indian pottery,

often found in the overarched niches formed by hollow squeeze-ups of lava, show that prehistoric Indians peopled the flow, at least around its borders. In 1540 the first party of white men to enter New Mexico, led by Coronado, crossed the lava bed en route to the Acoma Pueblo. Onate, in 1605, returning from his discovery of the Gulf of California, carved the earliest of the many Spanish inscriptions on the sandstone cliff at El Morro, where a dependable water hole attracted many expeditions. This spot, now a National Monument, is 13 miles west of the Ice Caves lobe of the lava bed.

The investigation here reported progressed intermittently from June, 1944, through the summer of 1948. From June to September, 1948, full time work was carried on from headquarters at the Navajo Fluorspar Mine four miles east of the Ice Caves resort.

The diversity of parent materials adjacent to the Grants Lava contributes to the region's edaphic interest, while the considerably more xeric climatic con-

ditions as lower elevations are approached bring about striking zonation of vegetation on the lava. This is apparently the only lava bed in the country any part of which has a water reservoir in the body of the lava, resulting in permanent ponds in the tube caves and sinks. These support a very rich flora and fauna, including some plants and a number of animal species not previously found in New Mexico.

The malpais habitats fall within two main divisions; the first comprises the steep volcanic cones, generally covered with loose ash except for the solid lava exposed at the summit and inside the crater. The second is the outspread flow, which is largely of the relatively smooth type called "pahoe-hoe" lava, although parts of the same flow may be extremely rough and jumbled at the surface, like the "aa" type. A flow may be subdivided into (1) flow surface, broken at intervals by the joints, shallow fissures, and deep fissures defined by Eggler (1941) for Idaho lava, versus (2) the major depressions caused (Henderson 1933) by the collapse of the roofs of tube caverns. These collapsed sinks either lead into confined pits, caves, and ice caves, or are open, well-lighted circular sink-holes and elongated troughs. All of the types of major depressions may be dry, or contain liquid water, usually as permanent ponds.

Primary succession on American volcanic deposits has been investigated by Griggs (1933) in Alaska and by Eggler in Idaho (1941) and Mexico (1948). Be-

cause the many different flows of the Grants bed have not been adequately dated by geologists, this area is less well suited to a study emphasizing primary succession. The aims of the present study are to (1) compare the three main plant communities on the flow surface, phytosociologically and climatically, and (2) describe the plant assemblages, and their controlling environmental factors, in the special discontinuous habitats both aquatic and terrestrial which diversify the area. Geiger (1950) and others have stressed the importance of microclimates. In such special habitats as ice caves and tube-cavern ponds the drastic differences from surface conditions render microclimatic study unusually significant. The negligible seasonal fluctuations give short-term factor observations much greater value than they would have in more ordinary habitats.

The nomenclature of vascular plants is that of Kearney and Peebles (1942). Herbarium specimens of the vascular plants are preserved in the writer's personal herbarium; others were retained by the specialists who identified them.

CLIMATE

Hooper (1941) published and discussed a table summarizing meteorological data before 1933, from five towns in the general region, including San Fidel, but most of these are too distant from the malpais for the present purpose.

The immediate vicinity of the Grants Lava Bed

TABLE 1. Temperatures at stations from high to low altitudes in the vicinity of the Grants Malpais, in degrees F.

Station	Altitude, feet	Years of Record	MEAN MONTHLY												Mean Annual
			Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
El Morro Airport . . .	7,120	8	24.9	20.9	24.9	44.0	52.5	59.5	66.6	65.9	58.7	47.7	34.7	29.4	45.8
El Morro National Monument	7,218	11	27.9	31.8	37.3	45.9	53.6	62.0	68.4	66.8	60.4	50.0	36.7	30.9	47.6
IX-XI Ranch	7,000	4	25.4	32.7	38.4	47.3	54.8	62.3	67.5	67.9	60.9	50.0	36.0	30.2	47.8
Grants	6,500	4	29.6	26.1	41.1	52.0	60.2	68.4	73.2	69.4	65.2	52.1	37.8	31.9	51.4
Acomita Airport	6,540	4	28.7	35.3	39.8	51.6	59.6	68.0	72.2	69.1	64.8	52.7	37.1	32.1	50.9
San Fidel	6,100	30	30.8	35.9	42.2	50.4	59.3	64.9	72.1	69.6	62.8	51.8	39.6	32.3	51.3

TABLE 2. Precipitation, in inches, at stations from high to low altitudes near the Grants Flow.

Station	Years of Record	MONTHLY												Total Annual
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
El Morro Airport . . .	8	0.46	0.54	0.87	0.54	0.49	0.61	1.79	3.01	1.30	1.04	0.30	0.81	11.76
El Morro National Monument	11	0.89	0.83	1.21	0.66	0.49	0.54	1.70	3.10	1.46	1.12	0.58	1.06	13.64
IX-XI Ranch	4	0.98	0.13	1.42	0.08	0.71	0.81	2.52	4.89	1.14	0.85	0.52	0.76	14.81
Grants	4	0.51	0.05	0.31	0.03	0.59	0.52	1.09	4.28	0.66	0.71	0.43	0.41	9.59
Acomita Airport	8	0.33	0.33	0.27	0.40	0.90	0.65	1.48	2.74	1.03	1.14	0.35	0.49	10.11
San Fidel	30	0.40	0.48	0.51	0.64	0.92	0.79	1.83	2.09	1.60	0.71	0.46	0.53	10.96

is now well provided with weather stations, at various altitudes (Fig. 1). That at San Fidel has been maintained for 30 years by the Franciscan Order, and one of 11 years standing is kept up at El Morro National Monument. The location of a transectinental airline route across the northern lobe of the malpais resulted in two more recent stations at the emergency airfields near El Morro and Acomita. Two others were established in August, 1945, at the IX-XI Ranch by Mrs. Lela McCord, and at Grants by the Forest Service. Tables 1 and 2 list these in order from high to low altitudes. The writer kept daily records of temperatures, precipitation, evaporation from an atmometer, and relative humidity from June 27 through August 31, 1948, at a standard Weather Bureau instrument shelter set up one mile inside the lava bed at Porter's Ranch, 3.5 miles from the IX-XI station outside the lava.

Only the San Fidel station has records of sufficient duration for the Weather Bureau (1930-1948) to calculate normal temperature and precipitation for months. The "Climatological Data" annual summaries tend to be incomplete for the other stations. From the detailed monthly reports, however, we have calculated presumptive normals for the five stations by determining the mean of all available data for each month at each station. The mean annual temperature in Table 1 is thus not the average of the few published annual means, but was obtained by adding the monthly means for each month separately for all the years of record, then averaging the resulting twelve monthly means. Similarly, the total annual precipitation given (Table 2) is the sum of the twelve monthly means for all the years of record.

The three weather stations at or over 7,000 feet in elevation show a decidedly lower mean annual temperature and higher annual precipitation than the three below that altitude. That the highest rainfall, nearly 15 inches, occurs at the IX-XI Ranch, east of the continental divide and considerably lower than the National Monument, may show the influence of the nearby lava bed.

Over the whole area the bulk of the precipitation comes in July, August, and September. At San Fidel 52 percent of the normal annual precipitation of 11 inches comes in these three months. These rains are sometimes torrential. After six months at San Fidel with a total of only 0.08 inch of precipitation, 2.08 inches fell during three days in July, 1944. Despite the high altitude of this region including the continental divide, and the proximity of the Zuni Mountains and Mt. Taylor, the terrain surrounding the Grants malpais has the general character of high plateau rather than mountainous land.

A comparison of the mean monthly temperatures for summer and winter indicates the wide range characteristic of a continental climate, even though the monthly means do not well reveal the annual range because of the very low minima on summer nights and the high maxima on winter days. The daily range of temperature is great at all six stations; a range of more than 50° F is not unusual

either in summer or winter. A wide daily range is typical of semi-arid high-altitude plateau regions.

Evaporation data were collected during the summer of 1948 at thirteen sites by means of Livingston white atmometer spheres. While nine of these sites represent special habitat conditions, the remainder are normally exposed sites both on and off the lava. The corrected, mean daily water loss at these four sites averaged 56.6 ml per atmometer during July and 49.6 during August. Although July and August were the two warmest months, they were also the two with the greatest precipitation.

LAVA FLOW SURFACE COMMUNITIES

At higher altitudes the malpais is forested, while its lower reaches support shrubby vegetation. The map (Fig. 1) shows the approximate limits of the three communities. The latter appear to be well stabilized, or adjusted to their respective climates in combination with the peculiar edaphic conditions of the malpais. The environmental resultant, in each of the two higher belts, supports a more mesophytic vegetation type than occurs on adjacent non-lava land. Therefore, the Douglas fir and ponderosa pine communities on the malpais are postclimax to adjacent non-lava communities. The low elevation Apache-plume type is preclimax to the ponderosa pine, and the latter is preclimax to the higher Douglas fir vegetation.

THE DOUGLAS FIR BELT

Under the relatively cool, moist conditions of the highest or northwest lobe, a stand of mixed Douglas fir (*Pseudotsuga taxifolia*) and ponderosa pine (*Pinus ponderosa*) covers eleven square miles. It is termed the "Douglas fir belt" because this tree is generally distributed through the belt, although in some portions the pine is more abundant.

Douglas fir occurs not only on lava (Figs. 2, 3), but also on the outside slopes of some of the cinder cones where it is entirely restricted to north slopes, and within the craters, especially the north-facing slopes on the craters' south sides. It is absent on level sites adjacent to the lava, where ponderosa pine predominates at this altitude. Douglas fir is very rare even on north slopes of non-lava kipoukas (islands surrounded by lava), and of hills adjacent to the lava. Nor is it as prominent in the Zuni Mountains to the north until altitudes at least a thousand feet higher are reached, and then only on protected sites.

Douglas fir is much less common on the smoother or ropy pahoehoe lava than on the much fragmented rough type around the edges of flows and in narrow tongues and upheaved ridges. *Pinus ponderosa* is favored by the smoother lavas in the Douglas fir belt, but most of this portion near the sources of the flow is rough. *Juniperus scopulorum* thrives in much-broken lava, while *J. pachyphloea*, more characteristic of cinder cones and non-volcanic soils, occurs on the smoothest flows, but uncommonly.

Sample plots were charted on the lava at various places in the Douglas fir belt within one mile west



FIG. 3. Mixed forest stand of the Douglas fir belt, near the Ice Caves.

and south of the Ice Caves Resort. These were in the form of strips one chain (66 feet) long by ten links wide, or ten times as long as wide. The north-south strips were laid out systematically one chain apart in an east-west direction. The method was to fasten down a surveyor's "chain" marked off in numbered links, then, with a light strip of wood ten links long, marked off in links, to work along one side of the chain from end to end, charting the plants on graph paper. Twenty-five such 1/100 acre sample plots were charted here.

Table 3 presents phytosociological data from the sample strips. Three of the plots, on much-broken lava, contained no plants except lichens. Douglas fir exceeds all other species in abundance (number of individuals per acre) and basal area, but *Juniperus scopulorum* shows higher frequency and greater cover because of its low sprawling form. The shrubby species are of such form and size as to be unsuited for determination of number of individuals or basal area of stem. Other plants, each with coverage less than 50 square feet per acre, are *Artemisia carruthii* (frequency 44), several grasses (52), two *Opuntia* spp. (16), and *Populus tremuloides* (14).

A striking fact is the complete absence of Douglas fir reproduction in the plots. The only tree seedling or sapling was one young ponderosa pine. Scarcity of tree reproduction is characteristic of the

lava surface generally, where difficulty of ecesis is extreme.

The more exposed Douglas firs have a thick, tapering trunk and short, low crown, resembling the Southern California mountain form of *Pinus contorta*. Many of the fir crowns are deformed or wind-trained by the prevailing westerlies. The species reaches a great age, but growth is very slow, and heights of 60 feet are seldom attained except in sheltered troughs. Often the wood of dead trunks shows a strong spiral twist in the grain. This trait is most evident on very rocky substrates. The higher part of the lava bed, with practically no soil visible, has trees with the most twisted grain. In some of the lava bed firs the vertical trunks show spirals so flat that the wood elements appear to run horizontally around the trunk's circumference (Fig. 4).



FIG. 4. Transverse grain in the lower trunk of a dead deformed Douglas fir on Recent lava.

TABLE 3. Analysis of lava species in the Douglas fir belt near the Ice Caves. Frequency in percent of plots sampled.

	Abundance (stems per acre)	Basal Area (sq. ft. per acre)	Crown Cover (sq. ft. per acre)	Frequency
Trees				
<i>Juniperus scopulorum</i>	24	31	3593	56
<i>Pinus edulis</i>	12	6	711	24
<i>Pinus ponderosa</i>	8	7	436	12
<i>Pseudotsuga taxifolia</i>	36	73	1930	36
Shrubs				
<i>Fallugia paradoxa</i>	—	—	122	48
<i>Forestiera neomexicana</i>	—	—	54	20
<i>Phyocarpus opulifolius</i>	—	—	1111	48
<i>Rhus trilobata</i>	—	—	217	48
<i>Ribes cereum</i>	—	—	42	36

Trees in narrow joints may mature although extremely dwarfed. A Douglas fir only sixteen inches high, growing in a crack about one-eighth inch wide, bore cones.

The following peculiar relation between plants and the surface geology has been seen only in the Douglas firs. While most lava squeeze-ups (Nichols 1939b) are bulbous and rounded, occasionally hollow linear ones are seen. These may be as much as 20 feet long, hollow, crooked, usually flattened tubes running horizontally. A root of a fir gets under the

surface crust and grows along the tunnel where warmth and moisture, but little or no soil, occur. As the tree grows, the root's older part, perhaps six inches or more in diameter, may crack the rock roof over it, heaving it up to expose many feet of the root's length, and make evident the previously inconspicuous or invisible squeeze-up formation.

A station was operated in lava one-half mile south of the Ice Caves Resort, from July 1 through August 30, 1948; white-bulb atmometer readings and air and soil temperatures were obtained. The atmometer, placed 3 feet above the general lava surface, lost an average of 60.2 ml daily during July, and 44.4 ml during August. The greater July loss in the Douglas fir than in the ponderosa pine belt is due to greater exposure to wind.

A simple, inexpensive method, apparently new, was used for securing simultaneous air and soil temperatures. An Air-guide "indoor-outdoor" thermometer has parallel scales and two columns. The "indoor" column is of the ordinary type, but the bulb for the "outdoor" column is a metal cylinder at the end of a flexible 56 inch cable. The air temperature was read from the "indoor" column, while the "outdoor" bulb was left buried 9 inches under the soil in thin shade among the roots of a juniper, as no unshaded soil of comparable depth is found in this habitat. Since the instrument does not record, it is useful only where frequent visits can be made.

Of the 62 daytime air-soil temperature readings in the Douglas fir lava, the maximum for both media came July 15 with air (in shade) 88° F, when the soil at 9 inches was 69° F. The maxima for August were 85° F for air and 63° F for soil. The minimum soil temperature in the two months was 57° F at 7:00 A.M. when the air temperature was 58° F. The mean daytime temperature for air in July and August together was 77.1° F; for soil, at 9 inches, 61.5° F.

A three-pen Foxboro recording thermometer was run from August 16-21 in a hemispherical hollow squeeze-up with one bulb exposed on the unshaded lava surface. The brass-colored bulb on the bare rock showed a mean temperature 21° F higher than that of the air in shade. The extent to which the black lava absorbs the sun's radiant energy is indicated by the maxima which were above 127° F on four of the six days. A great range of temperatures between day and night was revealed. For example, on August 18 the temperature fluctuated between 46.2° F and 129.2° F, a range of 83 degrees. Both the daily range and the extreme maxima must be major factors in limiting the pioneer vascular plants on the bare lava to a few species, mostly woody perennials. The maximum is closely related to the water factor, for obviously where such temperatures are attained most moisture within reach of roots of young seedlings would be evaporated.

The dominant species of lichen in the Douglas fir belt, as on the Grants flow generally, is *Parmelia neoconsersa* Gyeln.; but, on the finely fragmented black lava southwest of Flagpole Cone, *Parmelia dendritica* Pers. is the commonest lichen. Three other

members of this genus occur on lava at high altitudes. The surface of this high altitude part of the flow is less xeric than that of other parts at lower elevations, and it supports more variety of lichens and mosses. On the north sides of high lava pinnacles and the north-facing cliffs of the deep sink-holes, the yellow crustose *Acarospora evoluta* H. Magn. is conspicuous. *Ramalina pollinaria* (Westr.) Ach. and *Cladonia fimbriata* (L.) Tr. var. *simplex* (Weis.) Tr. occur on lava. On the dead lower branches of conifers one finds *Usnea variolosa* Mot., and *Parmelia caperata* (L.) Ach. var. *incorrupata* (Moore) Berry.

The highest elevation on the outspread flows, where Douglas fir and ponderosa pine now predominate, had a forest climate at the time the older flow was extruded. This is evidenced by the tree tubes in the weathered lava at the southeast base of Flagpole Cone. Figure 5 depicts a deep vertical cylindrical hole formed by magma flowing around a tree trunk eighteen inches in diameter. The tree tube ends at the top within a weathered rock chimney which is interpreted (Lindsey 1949a) as a tree-trunk squeeze-up. Within some of the tubes there are markings which are probably the rock molds of tree bark. The diameters and depths of the tubes also point to trees of the size of ponderosa pine or Douglas fir, rather than pinon pine or juniper. If, as Hooper (1941) suggests, this part of the flow "is likely of Miocene age," the trees may have been more mesophytic species grown on non-volcanic soil in a moist climate.



FIG. 5. The mouth of a tree-trunk tube in Miocene (?) lava, fossil evidence that the climate at the time of this flow permitted tree growth.

THE PONDEROSA PINE BELT

Below the Douglas fir belt the major vegetation cover of the malpais, the ponderosa pine forest, occurs. The best stands are found on the lava at, and not far within, its edges, where the moisture supply is relatively high due to drainage from the usually heavy soil that has washed against or over the lava's edges. The highly irregular borders of the exposed lava furnish an important edge effect, so that the largest and best pines for sawlogs are accessible to the lumberman. Many of these trees are twice the average height of those deeper in the malpais. Well back from the edges the slower growing pines often

show a broken dead stub at the top, combined with "heart-rot" in the trunk.

Whereas ponderosa pine is common in the Douglas fir belt, Douglas fir is absent over the greater part of the ponderosa pine belt. Both the upper and lower limits of the latter are quite irregular. The vegetation in the ponderosa pine belt was analyzed (Table 4) in typical unlogged portions by means of 15 quadrats, each one-tenth of an acre in area. Ponderosa pines over 4 inches DBH totaled 42 square feet per acre in basal area. Those of smaller size were included as reproduction. *Juniperus scopulorum* is much less prominent here than among the Douglas firs, while *J. monosperma*, which occurs in trace amounts in the fir belt, is slightly higher here with a crown cover of 11 square feet per acre. *J. pachyphloea* is occasional in the ponderosa pine belt, on very smooth flows, but was not included in the sample plots. The crowns of *Pinus edulis* cover only 7.5 square feet per acre, and *Ribes cereum* the same.

TABLE 4. Vegetational analysis in the ponderosa pine belt, based on 15 one-tenth acre quadrats.

	Abundance (stems per acre)	Cover (sq. ft. per acre)
Trees		
<i>Juniperus scopulorum</i>	1	25
<i>Pinus ponderosa</i>	3.3	1,084
<i>P. ponderosa</i> reproduction....	7	24
Shrubs		
<i>Fallugia paradoxa</i>	—	12
<i>Forestiera neomexicana</i>	—	240
<i>Quercus gambelii</i>	—	630
<i>Q. grisea</i>	—	251
<i>Rhus trilobata</i>	—	380

The most striking difference in the shrubby stratum is the substitution of *Quercus* for *Physocarpus*. Two species of oaks, which were not present in the Douglas fir sample plots, are conspicuous as thicket-forming shrubs in jumbled, blocky Tertiary lava. Low cacti cover 4 square feet per acre. *Yucca baccata* occurs occasionally.

Herbaceous cover is much better developed than in the Douglas fir belt. The most important species is the side-oats grama (*Bouteloua curtipendula*) which occupies 21 percent of the surface or 9,148 square feet per acre. It does well in rough lava in the sparse shade of the pines, and as a shallow crevice species in smooth lava. Where a thin soil has accumulated in shallow lava synclines, blue grama (*Bouteloua gracilis*) replaces it, covering 9% of the area within the sample plots, or 3,920 square feet per acre. In individual square-chain quadrats, this grass covers up to 80 percent of the surface. *Artemisia carruthii* var. *wrightii* ranks next, covering 810 square feet per acre. Other plants, each occupying less than 0.5 percent or 218 square feet per acre, are, in decreasing order of coverage, *Lotus wrightii*, *Verbena wrightii*, *Chrysopsis hispida*, *Eriogon divergens*, and *Berberis repens*.

The principal instrument station in the malpais (Fig. 6) was in the coarsely fragmented basalt of the ponderosa pine area, at 7,100 feet altitude, one mile within the lava bed. Data obtained by daily visits from June 27 through August 31, 1948, are summarized in Table 5.



FIG. 6. Meteorological station in the ponderosa pine belt, one mile within the lava flow.

TABLE 5. Weekly summaries of summer temperature and rainfall for 1948 at ponderosa pine Lava and IX-XI Ranch Stations, one mile within and outside the malpais, respectively.

	TEMPERATURE (°F)				RAINFALL (inches)	
	Lava Station			IX-XI Ranch	Lava Station	IX-XI Ranch
	Mean Max.	Mean Min.	Weekly Mean	Weekly Mean		
June 27-July 3.....	83	56	69	62	.04	0
July 4-10.....	88	57	73	67	.05	0
July 11-17.....	92	58	75	68	.04	0
July 18-24.....	82	57	69	67	1.39	1.30
July 25-31.....	85	55	70	67	.89	.39
August 1-7.....	86	58	72	67	.61	.77
August 8-14.....	83	55	69	63	1.07	.84
August 15-21.....	87	57	72	67	.35	.72
August 22-28.....	84	52	68	64	.16	.24
					4.60	4.26

A white bulb atmometer at the lava instrument site averaged, after correction, a mean daily water loss of 56.3 ml in July and 44.6 ml during August. The bulb was located on a post about three feet above the average surface level of the blocky lava. An open forest of ponderosa pine surrounds this station. Forty-six sling psychrometer readings were taken on as many different days there, all but nine in the forenoon. The range of relative humidity found was from 16 to 59 percent. During July the mean daytime relative humidity was 38.4 percent; during August, 47.5 percent. This difference is correlated with August's lower atmometer loss.

The recording thermograph was kept in the instrument shelter at this site for two weeks in 1948. The mean of hourly readings from June 28-July 5 was 68° F in the air of the shelter, 77° F under 3 inches of soil, and 65° F under 12 inches of soil. August

22-29 showed means of 67° F under 9 inches of soil. The daily range of air temperature was consistently greater during the August period, the greatest being 34° F. The greatest daily range at 3 inches in the soil was 27° F, but at 9 inches it was only 3.6° F. Under 12 inches of soil the range for the week was 2.7° F. The thermograph bulb lying on bare unshaded lava produced a very irregular record due to clouds passing before the sun. Its maximum was 142° F, and the greatest daily range 92° F.

The height of the water table in the ponderosa pine belt at this instrument site on Porter's Ranch, judging from the well at the ranch house, is about 205 feet below the lava surface, in August.

The composition of the ponderosa pine community may be explained in the light of experimental work. Pearson (1924) wrote regarding ponderosa pine seedlings, "Yellow pine² is most capable of supplying itself with water and is fairly immune to heat injury. Douglas fir is well equipped to obtain its water, but its leaves are most easily superheated." Bates (1923) goes so far as to say that Douglas fir "requires less moisture than yellow pine, or at least, that the moisture is not a controlling factor. . . ." He concluded from extensive experiments with potted seedlings that, in the ability to withstand drought, there is no essential difference between ponderosa pine and Douglas fir. Stressing the fact that the factors controlling seedling success must be considered as almost independent of those controlling later growth, he stated of Douglas fir, "Extended observation shows that it will grow almost anywhere that yellow pine will grow, provided only that the seedlings may have shade until they have passed the stage when most susceptible to heat injury," and concluded that temperature rather than moisture is the controlling factor. Several workers have pointed out that the surface soil on drying becomes the warmest part of a young seedling's environment, and that this is the point where the plant is most susceptible to injury from temperature and drought. Pearson (1924) found that wilting of fir and ponderosa pine seedlings was mainly in the nature of a collapse of the stem at the ground line. He brought out evidence that in nature it is the momentary maximum temperatures that determine the degree of injury, and showed that Douglas fir is much more sensitive than ponderosa pine at comparatively low temperatures under direct radiation. He stated "... it is evident that extreme heat, though of short duration and rare occurrence, may be an important factor in preventing reproduction generally and in drawing a line between the natural habitats of the different species. Where soil drying accompanies high temperatures, as it almost invariably does in nature, temperatures of only 130° F may do considerable injury." He concludes that "As between yellow pine and Douglas fir, the ability of the latter to replace the former depends almost entirely upon the critical temperature conditions which the germinating seedlings must withstand at the surface of

² The authors quoted here used the common name "yellow pine" for *Pinus ponderosa*.

the soil. It is known that Douglas fir and yellow pine seedlings have almost equal root vigor, and the distinction between the two is clearly due to greater tolerance of heat on the part of yellow pine."

Since no Douglas fir of any age and very few first year pine seedlings were found in the ponderosa pine belt, direct evidence such as heat lesions cannot be ascribed. However, accepting the conclusions of the workers quoted above leads to the explanation that the high lava-surface temperature, possibly in combination with the extreme daily range, is the primary factor excluding Douglas fir from the ponderosa pine belt. The lava surface is well insolated and undergoes rapid changes in moisture, fulfilling the conditions which, according to Bates, "... for the establishment of seedlings would appear to demand prompt germination and prompt deep rooting. Yellow pine is preeminently adapted to these conditions by reason of its large seeds, which produce large sturdy seedlings with a habit of immediate deep rooting. . . . Success is dependent on the roots reaching a layer of the soil which does not dry out dangerously through insolation." Ponderosa pine has a deep taproot with long laterals, while Douglas fir lacks such wide-ranging roots.

Like the Douglas fir belt, the ponderosa pine forest reaches much lower altitude on the malpais than on other lands. Along the road between the Ice Caves and Grants, this belt occurs seven miles farther downgrade on lava than on immediately adjacent granitic soils. Records from the IX-XI Ranch station, located in pinon-juniper vegetation opposite the ponderosa pine belt of the malpais, may be compared with our lava station: each station lies one mile from the lava's edge, outside and inside the flow respectively. Weekly summaries from both are given in Table 5. The mean temperature for the nine weeks at the lava station was 71° F while that at the ranch was only 66° F. The mean for every week was higher in the malpais. The ranch is 100 feet lower in altitude, which is hardly a difference of consequence, but if this had any effect it should tend toward higher temperatures at the ranch. The normal plant distribution is reversed, in that the lower temperature would be expected in ponderosa pine vegetation. It follows that temperature can be ruled out as the factor furthering extension of ponderosa pine to abnormally low elevations in the malpais. Table 6 compares Pearson's (1931) minimal values under which ponderosa pine grows in northern Arizona, and corresponding data from two permanent weather stations near the Grants Lava. Pearson considered climatic minima rather than maxima to be limiting. The five-degree difference in temperature for July-August between the ranch and the lava station indicates that the latter's June-September temperature would also be higher than those for the ranch and Acomita where pinon-juniper predominates. Given adequate moisture, then, ponderosa pine will grow under June-September temperatures with a mean higher than 65° F and a mean-maximum higher than 83° F. This supports Pearson's statement that "It is reasonable to believe that all

trees would grow better in higher temperatures than prevail in their natural habitats, if these temperatures were accompanied by sufficient rainfall" and his conclusion that the important temperature limitation is a low, rather than high, mean maximum during the growing season.

TABLE 6. Comparison of Pearson's minimal values for ponderosa pine in northern Arizona, with conditions at two stations near the Grants Lava.

	PRECIPITATION		TEMPERATURE, JUNE-SEPT.	
	Annual	May- Sept.	Mean air	Mean max. air
Northern Arizona....	20	9	58	70
IX-XI Ranch.....	15	10	65	83
Acomita.....	10	7	69	82

The 20 inch annual precipitation minimum given for Arizona ponderosa pine is 5.2 inches more than the normal year's precipitation at the IX-XI.

Larsen (1930) gives the range of mean annual temperature under which the ponderosa pine type is found in the northern Rocky Mountains as 44-50° F. Table 1 indicates that the El Morro region and the IX-XI Ranch come within this range, but fall far short of the minimum annual rainfall requirement of either Larsen or Pearson. Actually, very few ponderosa pines occur at these non-lava sites, and those chiefly in rocky gullies as on the Inscription Rock. The hot, dry Grants, Acomita, and San Fidel stations show mean annual temperatures only slightly above 50° F, but with precipitation of approximately 10 inches they scarcely support junipers. The mean annual temperature over much of the malpais ponderosa pine area is very probably equally high. Since none of the six weather stations shows a normal precipitation within 5 inches of the 20 inch minimum, it is apparent that favorable moisture conditions exist in the malpais, determined by either micro-climate or edaphic factors or both, which compensate for the unusually high temperature.

Local ranchers maintain that rain falls much more frequently over the black malpais than over the adjacent area. Mrs. McCord states that this was even more noticeable at Point of Lava, the southern extremity of the malpais, where she resided for many years, than at her IX-XI Ranch meteorological station. Yet, the broad valley where the flow lies would be expected, from considerations of topography, to receive considerably less precipitation than the higher mountain-studded plateau to the west, whence the storms come.

Table 5 shows that there was little difference in total amount of rainfall between the two stations, the rain gage in lava receiving only 0.34 inch more during these two wettest months of the year. However, its distribution differed markedly. On 15 days of the nine-week period it rained at the lava station

without raining at the ranch, whereas there was rain on only 4 days at the ranch without rain at the lava station. During the nine weeks, a total of 4.60 inches fell on 27 different days at the lava station, 4.26 inches on 16 days at the IX-XI Ranch, 4.23 inches at El Morro National Monument on 16 days, and 3.51 inches at El Morro Airport on 10 days. While figures for one rainy season are not conclusive, they support the observations of the local residents regarding the effect of the malpais on the frequency of rains. As regards amount of rainfall, longer records show that the IX-XI Ranch, 120 feet lower in elevation than the El Morro Airport, but much closer to the malpais, received during its 38 months of record a total precipitation which was 22 percent greater than the total at the airport for the same months. The lookout on the fire tower at Oso Ridge, who commands a broad sweep of the malpais, states that rainclouds are more common there than elsewhere, and that occasionally clouds will be filled in rather solidly over the lava when very few are to be seen over the surrounding country.

It appears that there are more frequent rains and possibly also a greater amount of rainfall on the malpais than at equivalent altitudes away from it, probably due to the dark basalt becoming hotter than non-lava rocks, consequently heating the air more by conduction and promoting more active convection over the flow than occurs over the surrounding land.

While rainfall differences may exist broadly as between the malpais and adjacent lands, it is certain that edaphic factors help determine the effectiveness of brief showers in particular and of the water factor in general. Due to the fractured nature of the basalt, rains, of amounts that would be insignificant on ordinary soils because of rapid evaporation and run-off, are doubtless more effective, since the water concentrates in the few crevices where the soil and plant roots also occur. For the same small investment in root surface a tree in the lava thus has access to much more moisture than would a tree in ordinary soil where the water is dissipated throughout the general soil mass and much more water is required to bring the soil above the wilting percentage. Moreover, the precipitation falling on the rough, fissured lava runs in instead of running off. In contrast, adjacent lands contribute much run-off to the malpais, which becomes available for the lava border plants and for the sub-lava reservoir.

Along the western edge of the malpais are extensive high plains of older lavas, covered with a heavy soil of varying thickness bearing generally a cover of shrubby composites and xeric grasses, with a scattering of Junipers. Ponderosa pine not only occurs on the younger lava flow, but wherever to the west of it a buried ridge of older lava comes near or breaks through the soil surface, isolated groups of ponderosa pines present themselves. It is no exaggeration to term the species an indicator of basalt rock in this area (Fig. 7).

On the east side of the flow, under the great sand-



FIG. 7. Tertiary flow nearly obscured by loess, showing the relation between ponderosa pine and the still exposed ridge-tops of rough lava.

stone cliffs at "The Narrows" nineteen miles south of Route 66, is a pure stand of remarkably stunted *P. ponderosa* (Fig. 8) growing under extreme con-

ditions on pahoehoe lava, at approximately 6,800 ft. elevation. None of these trees exceed fifteen feet in height. One of the larger ones had averaged 0.2 mm annual radial growth. These trees are very contorted and deformed, some having the trunk arched over so that its upper portion lies prostrate. In contrast, ponderosa pines on sandstone adjacent to the edge of the flow have developed normally. The lava forms suggest timberline trees, yet there is no consistent orientation or wind-training effect. The deformation and dwarfing are apparently caused by an unfavorable combination of factors in a habitat far too xeric for normal growth, but without competitive species.

THE APACHE-PLUME BELT

The ecotone between the ponderosa pine belt and the belt dominated by Apache-plume (*Fallugia paradoxa*) is characterized by a mixture of shrubby veg-



FIG. 8. Stunted stand of ponderosa pine at its lowest elevation on lava, at the Narrows at the southeast edge of the flow.

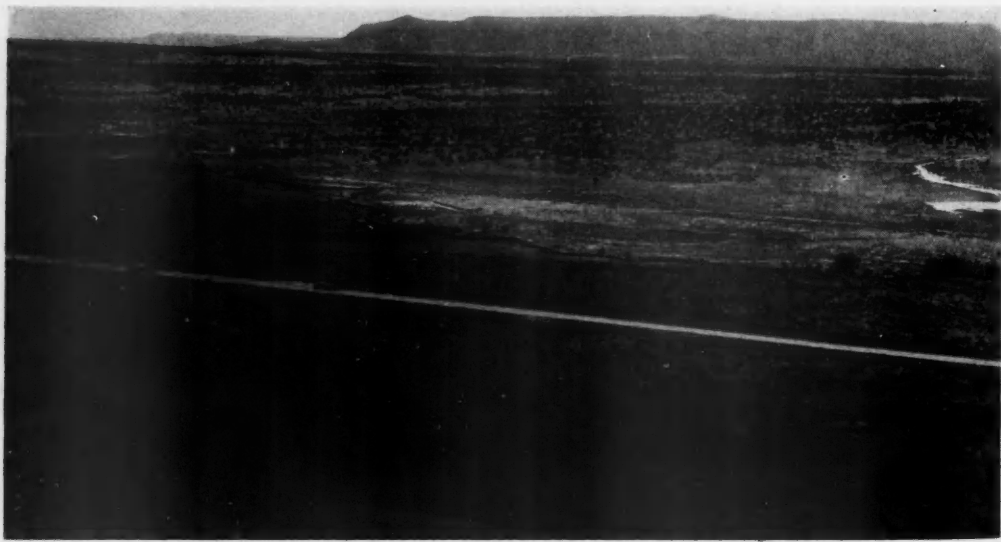


FIG. 9. General view of narrow lava tongue along the Rio San Jose, Acoma Indian Reservation, representing Apache-plume vegetation on pahoehoe lava between the Rio San Jose and the Santa Fe main line. Highway U. S. 66 is shown also.

etation with low trees, principally piñon (*Pinus edulis*) and *Juniperus monosperma*. These two species are dense enough to give this broad transition a distinct woodland physiognomy. Here the lava surface, especially the Tertiary material on the west edge, shows the densest lichen growth; species of the *Parmelia conspersa* group practically cover the rock. At elevations somewhat below this mixed vegetation, piñon is absent; one-seeded Juniper, a more xerophytic species than the *J. scopulorum* of the two higher belts, is much scarcer, but scattered, stunted individuals occur even on the low end (Fig. 9) of the recent flow.

Table 7 lists the principal species of the typical vegetation in the Apache-plume belt, with data on cover and frequency based on 25 plots each 100 by 10 links. These include several series of plots separated by one-chain intervals, in different parts of the flow where vegetation occurs. The lava terrain is rather sharply divided into relatively smooth pahoehoe lava, broken at intervals by large deep fissures, and extremely rough aa-type material with small loose fragments making an unstable substrate very porous to water. The latter type is practically devoid of any plants except lichens. Table 7 is based on the vegetation of the lower reaches of the recent lava where vascular plants occur; the bare areas of the aa-type lava, covering approximately one-sixth of this belt, are excluded. The chief grass is *Bouteloua gracilis*; the few other grass species combined have abundance (30) and frequency (32) values similar to it. *Forestiera neomexicana*, common on the lava surface in the Douglas fir belt, here is confined to moist marginal depressions and filled sinks.

TABLE 7. Lava vegetation in Apache-plume belt, based on 25 one-hundredth acre quadrats. Cover, square feet per acre.

	Cover	Frequency
<i>Artemisia wrightii</i>	144	52
<i>Bouteloua gracilis</i>	27	28
<i>Brickellia californica</i>	297	40
<i>Chrysopsis hispida</i>	177	56
<i>Fallugia paradoxa</i>	2,562	92
<i>Opuntia arborescens</i>	45	24
<i>Ribes cereum</i>	26	12
<i>Rhus trilobata</i>	360	32

The climatic data from the San Fidel, Acomita, and Grants weather stations (Tables 1 and 2) provide a close approximation of conditions in the Apache-plume belt. The attenuated northeast lobe of malpais is so narrow that no local increase in rainfall, above the 10 inch average of the stations, is likely. Indeed, the vegetation gives every evidence of more xeric conditions on the recent lava than on either the adjacent old lava or non-lava lands. This is not surprising in view of the temperature, which exceeds the 51° F annual mean of the three weather stations because of heat absorption and conduction by the dark basalt, less protected by plants than in the two forested belts. Even on the lava tongue

paralleling the Rio San Jose where the water table is only twelve feet beneath the general lava surface, Junipers are scarce and slow growing, nor is there any apparent benefit to the various shrubs. Two miles south of the stream where the water level in an Indian well alongside the flow shows a water table, in August, 49 feet below the higher parts of the lava, *Fallugia* grows as well as anywhere. It is likely that this shrub vegetation is not dependent on the subsoil water reservoir, but on surface water collected in joints and soil-filled crevices. No roots of the surface plants were ever found extending down to the water of crevices or pit-ponds.

A white-bulb atmometer 2 feet above the general lava surface in this belt averaged 63 ml water loss per day from July 8 to 17, indicating a very high evaporating power for this habitat. In another part of this belt, 60 ml was evaporated daily, on the average, from July 30 to September 1. The effect of the rainy season on relative humidity is illustrated by the 4 percent humidity on May 12, before its onset, compared with 19 percent on July 17, both days being cloudless.

The plant habitats on pahoehoe flows in Idaho were classified in four types by Eggler (1941). The plants of the Grants lava Apache-plume belt, where the very broken lava is essentially sterile, conform fairly well to these habitat types. *Chrysopsis hispida* especially, and *Artemisia* spp. tend to be restricted to the narrowest cracks or joints. *Bouteloua gracilis* is a joint plant in early successional stages, while on old, soil-covered lava it is the climax species among scattered *Juniperus monosperma*. Apache-plume is primarily a joint species which is common in the shallow-crevice habitat also. *Rhus trilobata* var. *anisophylla* is most typical of shallow crevices, and *Brickellia californica* belongs in this category. Crevices more than two feet deep support *Ribes cereum*, *R. inerme*, and *Pericome caudata*. The latter illustrates how a species changes its habitats in response to the varying xerism of different vegetation belts; it is a deep-crevice plant in the Apache-plume belt, but a shallow-crevice plant in the higher belts. *Ribes cereum* is found occasionally on very rough lava where the rugged terrain promotes conditions equivalent to those of deep crevices in pahoehoe lava. A similar relation obtains in the Douglas fir belt, where *Physocarpus monogynus* is abundant in shallow crevices on smooth lava and is the shrub most characteristic of very broken surfaces.

In vertical photographs of the lava surface in this belt, made by sending a Leica camera aloft about 110 feet suspended from two captive 50 inch Darex N4 balloons filled with hydrogen, the joint species blue grama and *Chrysopsis hispida* form an irregular, more or less broken reticular pattern; along its lines shrubby species occur at intervals. The use of such inexpensive spherical balloons is not satisfactory for balloon quadrat photos, since they are very difficult to control in even a slight breeze.

Lichens are well represented even in the lowest lobe of the flow, but tend to be restricted to the north faces of even small irregularities. The com-

TABLE 8. Plants most characteristic of the lava surface vegetation belts, and other volcanic and non-volcanic substrates adjacent to the Grants Lava.

SPECIES	Apache-plume Lava	Yellow Pine Lava	Douglas Fir Lava	Lava Cones	Cinder Cones	Cinder Bench	Granite Hills	Yellow Sandstone	High Tertiary Plains
<i>Actinea richardsonii</i> var. <i>floribunda</i>				+					
<i>Agastache neomexicana</i>				+	+				
<i>Allium cernuum</i>					+				
<i>Androsace septentrionalis</i> var. <i>glandulosa</i>				+					
<i>Aplopappus spinulosus</i> var. <i>typicus</i>	+								
<i>Arabis fendleri</i>			+	+	+				
<i>Arenaria confusa</i>				+	+				
<i>Artemisia carruthii</i> var. <i>wrightii</i>	+	+		+					
<i>Asclepias tuberosa</i>					+				
<i>Atriplex canescens</i>	+								
<i>Bahia dissecta</i>						+			
<i>Berberis repens</i>		+			+				
<i>Bouteloua curtipendula</i>		+							
<i>Bouteloua gracilis</i>	+	+	+						+
<i>Brickellia californica</i>	+								
<i>Castilleja integra</i>			+			+	+		
<i>Ceanothus fendleri</i>						+			
<i>Cercocarpus brevifolius</i>							+		
<i>Chenopodium fremontii</i>	+								
<i>Chrysopsis hispida</i>	+	+	+				+		+
<i>Cirsium megacephalum</i>					+				
<i>Cryptantha jamesii</i> var. <i>cinerea</i>						+			
<i>Chrysothamnus Greenei</i> var. <i>filifolius</i>									+
<i>C. nauseosus</i> var. <i>pinnatifolius</i>									+
<i>Descurainia pinnata</i> var. <i>halictorum</i>					+				
<i>Erigeron divergens</i>		+			+				
<i>Erigeron jamesii</i>	+				+				
<i>Fallugia paradoxa</i>	+	+	+						
<i>Festuca arizonica</i>						+			
<i>Forestiera neomexicana</i>		+	+						
<i>Frasera speciosa</i>						+			
<i>Geranium atropurpureum</i>						+	+	+	
<i>Geranium fremontii</i>			+						
<i>Gilia aggregata</i>					+	+			
<i>Gilia haydenii</i>					+				
<i>Hesperandanthus linearifolius</i>					+	+			
<i>Hymenopappus robustus</i>									+
<i>Juniperus monosperma</i>	+					+			
<i>J. pachyphloea</i>					+	+	+	+	
<i>J. scopulorum</i>		+	+						
<i>Lappula redovskii</i>						+	+		
<i>Lithospermum multiflorum</i>						+	+		
<i>Lotus wrightii</i>		+				+	+		
<i>Marrubium vulgare</i>						+	+		
<i>Mirabilis oxybaphoides</i>	+								
<i>Muhlenbergia montana</i>						+			
<i>Oenothera caespitosa</i> var. <i>marginata</i>					+			+	
<i>Opuntia arborescens</i>	+								
<i>Pentstemon linarioides</i>						+		+	
<i>Pentstemon trichander</i>			+						
<i>Pericoma caudata</i>	+								
<i>Phacelia intermedia</i>					+				
<i>Phaseolus angustissimus</i> var. <i>latus</i>					+	+			
<i>Physocarpus monogynus</i>		+							
<i>Pinus edulis</i>		+	+		+	+	+	+	
<i>P. ponderosa</i>		+	+	+	+	+	+	+	
<i>Populus tremuloides</i>			+		+				
<i>Portulaca retusa</i>	+								
<i>Pseudotsuga taxifolia</i>		+			+				
<i>Pteridium aquilinum</i>					+				
<i>Quercus gambelii</i>		+			+				
<i>Q. grisea</i>	+						+		

TABLE 8 (cont.)

SPECIES	Apache-plume Lava	Yellow Pine Lava	Douglas Fir Lava	Lava Cones	Cinder Cones	Cinder Bench	Granite Hills	Yellow Sandstone	High Tertiary Plains
<i>Rhus trilobata</i> var. <i>anisophylla</i>	+	+	+						
<i>Rhus glabra</i>									
<i>Ribes cereum</i>			+			+			
<i>R. inebrians</i>	+								
<i>Selaginella rupicola</i>				+					
<i>Silene laciniata</i>					+	+			
<i>Sitanion hystriz</i>			+		+	+			
<i>Solanum rostratum</i>	+								
<i>Sphaeralcea incana</i>	+								
<i>Tetradymia canescens</i> var. <i>inermis</i>									+
<i>Teucrium occidentale</i>	+								
<i>Thalictrum fendleri</i>					+				
<i>Verbena wrightii</i>	+	+					+		
<i>Woodсия plumerae</i>			+	+					

monest lichen in this belt is *Parmelia neoconspecta* Gyeln., *P. novemericana* Gyeln., *P. caperata* (L.) Ach., and *P. soredica* Nyl. Additional rock lichens are *Dermatocarpon minutum* (L.) Mann., *Acarospora texana* H. Magn., *Caloplaca bracteata* (Hoffm.) Jatta, *Aspicilia* sp. and *Physcia* sp.

In shallow and deep crevices, beneath shrubs, and in sink-holes occur five species of mosses, of which the first three are typical xerophytes: *Grimmia arizonae* Ren. and Card., *Tortula bartramii* Steere, *Orthotrichum anomalum* Hedw., *Homomallium mexicanum* Card., and *Leskea tectorum* (A. Braun) Lindb.

SUBSTRATES AND PLANT DISTRIBUTION

In addition to the three major vegetational areas on the lava, the unconsolidated volcanic deposits and the bedrock types of kipoukas and interdigitating marginal rocks provide different environments which affect plant life largely through physiography and the water factor. Table 8 gives the substrate type or types where each listed plant is at least highly characteristic, and in many instances, occurs nowhere else, in the general region of the Grants Flow. The influence of the parent materials is profound there because the soil mantle is either lacking or very immature over much of the non-lava, as well as the lava, terrain.

The first three columns of Table 8 indicate the flow surface plants; they do not show the species which are characteristic of special habitats such as dry or ponded sinkholes, ice caves, volcanic cones or loose ashy deposits within the general boundaries of the three altitudinal belts. Even though both age and character of surface may help determine plant cover, each of the first three columns includes the exposed portions of Tertiary to Recent flows, both rough and smooth.

The old, probably Tertiary, lava field at the north

base of Deer Mountain shows one long continuous depression where a tube cavern had collapsed. When Flagpole Cone erupted long afterward, a tongue of the Recent lava flowed up into the collapsed tube for about 0.3 mile, in the reverse direction from that of Deer Mountain's flow at this point. This narrow tongue of black, rough, soilless lava is densely covered with *Populus tremuloides*, while the weathered old surface just adjacent supports a very thriving stand of *Pinus ponderosa*.

The habitats designated in the third through ninth columns (Table 8) are all within essentially the same altitudinal range, so that altitude may be ruled out as a factor bringing about the differences of plant distribution shown by this part of the table.

The distinction between "lava cones" and "cinder cones" depends on whether solid or loose deposits cover the outer slopes of the steep central cone surrounding the crater. Since solid basalt apparently forms the basic structure around the crater of all the cones, cinder cones may show some exposed lava as steep cliffs facing the crater; Flagpole Cone (Fig. 2) illustrates this. Lava cones are few. Deer Mountain (Fig. 10) with its eroded summit, broad base, and gentle slopes represents this type. It is thinly covered with loess with a pH of 6.6 and 12 p.p.m. of nitrate nitrogen.



FIG. 10. A Tertiary lava cone supports ponderosa pine, while composite shrub dominates the flat lava plain at its base.

"Cinder bench" is applied, for lack of a better term, to flat areas, gentle slopes, and low ridges surfaced by volcanic ash. It comprises the loose volcanic deposits other than cinder cones. Due to the porous texture, there is little run-off or indication of water erosion on cinder benches, or even on the steep cinder cones.

The "Granite Hills" column represents the rough hilly land north of the Grants-Ice Caves road in the vicinity of the Navajo Fluorspar Mine. The fine-grained pink Pre-Cambrian granite is frequently exposed due to the steepness of slope. Its disintegration yields a heavy red clay showing a pH of 6.6, nitrate nitrogen of only 1 p.p.m. and a wilting percentage of 24. Measured at two-week intervals during July and August, it never showed a positive figure for available water at either 9 or 18 inch levels. Roots of the piñon-juniper cover seldom if ever go deeper than 18 inches.

The "yellow sandstone" constitutes some small kipoukas in the Douglas fir belt, providing a sharp contrast in flora with the adjacent Recent lava and cinder bench substrate types.

Not included in the table are kipoukas of red shale, and others of limestone. Both support piñon-juniper vegetation. The lower land of an extensive limestone kipouka south of Porter's ranch (at upper K, Fig. 1), supported a stand of tall, dense, luxuriantly fruiting *Bouteloua gracilis* in August, 1948. The owner, who grazes cattle there each winter, stated that this growth far surpassed that of any of the previous nine years. The nearest weather station (IX-XI Ranch) had recorded over 2 inches of rain, instead of the normal 0.8 inch, for June.

The "high Tertiary plain" (Table 8) comprises the area of buried old lava lying west of the continental divide between the Ice Caves and El Morro, and the area south of the divide with many large cinder cones shown in Figure 1. This is part of an extensive plateau country. Sand from disintegration of Morrison sandstone, with a pH of 6.4 and 2 p.p.m. of nitrate nitrogen, covers the old lava in the first-mentioned part, and fine textured soils predominate in the second (Fig. 11, foreground). Shrubby composites, especially *Chrysothamnus* spp., and grasses dominate the open scenery.



FIG. 11. Contact between the flat Tertiary plain at the continental divide and the steep edge of the Recent lava that overrode it.

Perhaps the most striking fact to emerge from Table 8 is that 41 of the 76 plants are characteristic of only one substrate category. None of the 41 is a tree; they are largely herbs. A group of 21 is characteristic of two categories only, so that only 14 are shared as characteristic species among three or more of the nine substrate types. Inasmuch as the differences between the last seven types cannot be ascribed to altitudinal differences determining diverse climates, and none of the habitats are well provided with organic content (or even much real soil, except for the Tertiary plain) probably their strong selective effect on plants is due largely to the considerable texture and porosity differences influencing water relations of the plant's roots in different ways.

Curiously, the strongest similarity in the characteristic plants, outside on the flat lava flow surface, is found between the granite hill and the cinder bench. It might be expected that the latter's vegetation would be most closely similar to that of the

cinder cone since the parent material is chemically identical or similar. On the contrary, there is twice as much resemblance between the granite hill and cinder bench flora as between the cinder bench and cinder cone. The effect of the residual clay of the granite hills and the fine loess component of the cinder bench may be similar enough to account for this.

The cinder cone has the most distinctive flora. Of the 17 herbaceous species listed, 11 were characteristic of this habitat only. The porosity and instability of the dry surface ash on a slope of approximately 54 percent imposes special conditions for plants during germination and ecesis.

To compare the growth of ponderosa pine on various lava and non-lava habitats, annual ring measurements were taken from 91 stumps on five types of sites, at altitudes high enough for this species to grow on non-lava substrates. Two age-intervals were used based on the age of the tree when the wood was laid down regardless of the chronological date. The radius increment was measured for a 50 year growth span, and where possible, also for a 100 year span, both beginning at age 25. Since random selection of stumps of all ages over 75 years was made, differences due to cycles of wet and dry years should largely cancel out. The oldest tree found was 370 years. Most rapid growth took place in trees on a cinder bench site—Cinder Hill—where the roots were strictly confined to a surface soil horizon averaging only 15 inches deep. These trees showed a mean ring width of 2.26 mm from age 25 to 75 years. Other rates are compared in percent of that standard. From age 25-125 the same trees averaged 77 percent. On lava in the ponderosa pine belt, the mean growth rate during the younger age interval was 72 percent, during the older, 60 percent. On the steep west slope of a lava cone the means were practically identical with those from the flat lava flow, 72 and 61 percent. Trees on a low sandstone kipouka showed 47 percent for the 25-125 year interval. On the pink granite hills the rate was 38 percent for the short interval, and 39 percent for the long, which correlates with the high wilting percentage and low available water in the clay soil, mentioned previously.

Alligator-bark Juniper (*Juniperus pachyphloea*) is the common tree which is most influenced in its distribution by the substrate factor. It is not found on lava (except rarely on smooth Tertiary flows in the ponderosa pine zone) nor lava cones, but occurs on the cinder cones, often near the summits, and less frequently on cinder benches and granite and sandstone slopes. In contrast, *Juniperus scopulorum* is characteristic of lava flows only, especially their portions in the Douglas fir zone. Since *J. monosperma* reaches the lowest altitudes in the Apache-plume zone, it is concluded that it is the most xerophytic of the three Junipers, *J. pachyphloea* intermediate, and *J. scopulorum* least xerophytic.

Fallugia paradoxa, which is by far the most important shrub of the Recent lava, is remarkably restricted to the lava flow. It was not found on any other substrate type even in the immediate vicinity

of the flow's edge, except for a very few occurring on the north slope of Flagpole just below the summit.

Two very similar species of *Geranium* are mutually exclusive in substrate distribution. The white-flowered *G. fremontii* grows only on Pleistocene or Recent lava flows in the Douglas fir belt. The purple-flowered *G. atropurpureum* occurs commonly at the same altitude and in close proximity to its relative, but never on lava of any age. It inhabits sandstone kipoukas and coarse cinder substrates. A comparable distribution obtains in the two common species of *Pentstemon*; *P. trichander* occurs only on the Douglas fir zone lava, while *P. linarioides* is seen only on sandstone and cinder bench sites.

This description and comparison of the substrate types furnishes a basis for a fuller account of two of them, the cinder bench and the cinder cone habitats.

CINDER BENCHES

The flat or rolling cinder sites studied were those in the vicinity of the Ice Caves, especially just north to east of Flagpole Cone. The loose volcanic deposits there were thrown out from the craters of Flagpole and the closely clustered cones southeast of it; they often occupy the space between a cone and a younger lava flow in a valley.

The instrument station at Cinder Hill was maintained on the flat top (Fig. 12) of a low east-west ridge of volcanic ash just across the road north from Flagpole Cone. This ridge is surfaced throughout by volcanic ash; a cinder pit at the high point of the road 100 feet below the summit shows that the cinder deposit here exceeds a depth of 20 feet.



FIG. 12. Transect area on Cinder Hill, showing *Muhlenbergia montana* and ponderosa pine.

This deposit consists, except for its surface horizon, of coarse, sharp, unweathered black clinkers generally from $\frac{1}{4}$ to $\frac{3}{4}$ inch in size, and forming a mass which is extremely pervious to water and air. The same material is found at a depth of three feet on Flagpole Cone. Its upper limit is very sharply defined; above the black clinkers is a finer textured tan-colored layer of weathered cinders mixed with fine windborne material. This soil-like layer, measured in 55 pits on the level top of Cinder Hill,

averages 15 inches in thickness. Ponderosa pine stumps there showed that radial growth had surpassed that found elsewhere. Between the trees is a profuse growth of the bunchgrass mountain muhly (*Muhlenbergia montana*). The roots of none of the plants extend into the underlying black clinkers, so that all the soil moisture taken up by plants is secured from the well-defined upper 15-inch mantle of soil.

A belt transect two chains wide and totaling 24 square chains or 2.4 acres along the top of Cinder Hill was charted on graph paper. The stand is a practically pure forest of scattered ponderosa pine, averaging 19.6 trees per acre. Their basal area at 4.5 feet above ground is 19.4 square feet per acre. The crown cover of this species is 2,565 square feet per acre, or 5.9 per cent of the area.

Increment borings from 21 of these living pines reveal a maximum radial thickness of the annual layer as 3.0 mm during the previous 50 years, when their mean radial growth rate had been 1.7 mm. The cores, kindly collected in December by Mr. D. Candelaria, showed that the mean growth rate during 1948 had been 1.6 mm, and therefore that the season of this study had been a normal growing season in terms of the previous half century. The two periods of best growth during the last fifty years were 1931-1934 and 1941-1944. Those of poorest growth were 1900-1904 and 1922-1928. Ages ranged from 69 to 130 years, the mean being 88 years.

The bunch grass clumps were measured two inches above ground in 20 systematically spaced four-thousandth-acre quadrats within a trenched treeless square chain of almost pure mountain muhly. The basal area of the grass cover amounts to 5,554 square feet per acre, or 12.7 percent of the surface area. The oven-dry weight of the grass tops above the two inch line is 462 lb. per acre. Quadrats laid out similarly in the portions of this ridgetop transect dominated by ponderosa pine gave basal area measurements for the grass of 1,208 square feet per acre.

The underlying black cinders at 18 inches, with a wilting percentage of 4.7, had no available water on five tests from June 30 to August 1. From 0.3 to 5 percent available water occurred on August 18; its absence until this late date must be a chief deterrent to root growth in this rootless horizon. The surface silt-cinder mixture at 9 inches contained 3 to 7 percent available water shortly before the rainy season, stored over the winter; but the percentage dropped to 0 in mid-July while absorption by roots was rapid. This occurred in both the trenched grass plot and in the ponderosa pine stand, and in both, the available water was restored to 11 percent by August 18. Evidently the thriving mountain muhly cover and the tree stand are limited by water supply during July, and the two communities consume approximately equal quantities of water.

A white bulb atmometer 15 inches above the ground among the mountain muhly clumps in the treeless trenched area lost from July 1-31 a daily average of

53.9 ml, while it averaged 47.0 ml during the first ten days of August. A rain gage at this station, at approximately 7,950 feet in altitude, caught 5.40 inches during July 21-August 31, 1948. The annual precipitation probably exceeds three times this amount. At the 7,100 foot station in the ponderosa pine belt eight miles southeast, 3.49 inches fell during the same period.

The earth-star, *Geaster* sp., is very abundant on the south slope of Cinder Hill; this fungus was found nowhere else.

CINDER CONES

All the cones on or near the Grants Lava Bed are situated on the western portion of the flow and on the adjacent area west of the flow (Fig. 1). On nearly all of these cones, the surface available for plant growth is largely volcanic ash. When unweathered, this material is very black in color, but the dry surface material ranges from dark to rather light gray, or sometimes reddish.

Douglas fir is typical of the north outer slopes (Fig. 13) of cinder cones near the Ice Caves, and of the north-facing slopes within craters. On cones it is accompanied by more ponderosa pine than in the fir belt on the malpais.



FIG. 13. North slope of Flagpole Cone, site of a belt transect from base to summit. Douglas fir on the outer slope is restricted to this narrow sector on the north side.

Some cones display bare cinder slopes on the outer south face, but most of them support trees. The outer slopes of a typical cone within five miles of the Ice Caves have piñon-juniper woodland on the south side, ponderosa pine on the east and west, and a Douglas fir-ponderosa pine mixture on the north exposure. More xeric cones at lower altitudes farther south show piñon-juniper on all sides except the north where a narrow sector of ponderosa pine, without Douglas fir, is maintained. Cones still farther down from the continental divide have piñon-juniper on all slopes, but denser on the north.

Flagpole Cone (Figs. 2, 14) also called Cerra de la Bandera, was investigated the most fully. A white atmometer bulb on the 53 percent south slope was 14 inches above the completely bare, unstable cinders. There, at an elevation of 8,090 feet, water loss was 60.2 ml daily from July 22 through August

31, 1948. The lowest relative humidity found at this station was 19 percent, on July 14.

Along the south base of Flagpole, barely on the cone's slope, extends a very scattered colony of the large-flowered *Oenothera caespitosa*. The bracken fern (*Pteridium aquilinum*) is the most abundant plant on the south and southeast slopes, often forming dense stands of foot-high fronds. It spreads by long rhizomes. Its sharp upper limit adjoins the bare ash of the upper slope (Fig. 14).



FIG. 14. Abrupt upper limit of woody plant cover and the bracken fern ground cover on east slope of Flagpole Cone.

A belt transect was charted 14 chains (924 feet) long by two chains wide on the slope from the north base of Flagpole Cone (Fig. 13) to its summit. The data in Table 9 show that of all plants, regardless of life form, ponderosa pine is predominant; it is represented in every unit but the highest one and shows by far the greatest total cover of all species. Douglas fir is found on only a narrow extreme northern sector of the conical volcano estimated as 10 or 15 degrees of the circle; here it is obviously just within its critical point for successful reproduction on this volcanic ash "soil" type. It is not found on the gentle slope just below the steep cone, where ponderosa pine is common. Douglas fir is barely represented in the lowest square of the steep transect. It showed no reproduction above unit D, and the sole mature specimen occurring in unit E was the highest on the cone. The best development is in unit C. Both young and mature trees appear quite normal, which is generally not true for this species on the lava surface. At this north slope station among the aspen, Douglas fir, and ponderosa pine the white bulb atmometer showed an average water loss of 47.6 ml per day during July, and 30.1 during August, the lowest rate in any tree habitat measured. This fact goes far to explain the good form and reproduction of the Douglas firs. The cinder soil at 9 inches has a nitrogen content of 3 p.p.m., the same as that of the unvegetated south slope station. The wilting percentage is about 4 percent on both slopes. The greatest available water during the summer at 9 inches in cinder cone soil was 10 percent in mid-August on the south slope and 6 percent on the north. This contrasts with the 2 percent maximum for July and August at the pon-

TABLE 9. Analysis of cinder vegetation in belt transect from base to summit of north slope of Flagpole Cone. "A" is the lowest of seven units of four square chains each; "G" includes the cone's summit. Individuals per acre, basal area (from DBH) and crown cover in square feet per acre. Reproduction—trees under 4 in. DBH.

	A	B	C	D	E	F	G
<i>Pinus ponderosa</i>							
Abundance.....	30	127	27	175	50	10	0
Basal Area.....	22	34	58	53	24	2	0
Cover.....	1753	3826	5388	3830	2163	625	0
<i>P. ponderosa</i> reprod.							
Abundance.....	160	115	347	247	80	10	0
Cover.....	430	5190	939	464	576	97	0
<i>Pseudotsuga taxifolia</i>							
Abundance.....	12	20	...	5	2.5	0	0
Basal Area.....	12	13	0.4	...	0.3	0	0
Cover.....	1318	1120	422	169	110	0	0
<i>P. taxifolia</i> reprod.							
Abundance.....	27	25	60	32	0	0	0
Cover.....	43	75	409	232	0	0	0
<i>Populus tremuloides</i>							
Cover.....	+	+	1568	1220	170	0	0
<i>Pinus edulis</i>							
Abundance.....	0	0	0	0	2.5	20	5
Cover.....	0	0	0	0	98	487	8
<i>Quercus grisea</i>							
Abundance.....	12	10	...	10	7.5	0	0
Cover.....	15	15	...	77	138	0	0

derosa pine weather station, where the nitrogen content is 15 p.p.m. The three-pen recording thermograph among the Douglas firs gave the data for soil temperatures in Table 10. The temperatures at the south slope station differed little from these at the 3 inch level, but averaged 9° F higher at 18 inches.

In unit A at this cone's base, *Berberis repens* and *Prunus virginiana* are abundant. In C occurred a solitary individual of *Pteropora andromedea*, the only one of this or any species of non-green angiosperm found. *Allium cernuum*, *Gilia aggregata*, *Silene laciniata*, and *Thalictrum fendleri* are the principal herbs in units A and B. Together with the conifer litter, these help to obscure the cinder surface. The latter is not really stabilized anywhere on this cone's 30° slope, and slides readily from beneath the feet. Although mature ponderosa pines are found higher than unit D, no appreciable amount of

TABLE 10. Soil temperatures (°F) at three depths on north slope of Flagpole Cone, July 13-August 1, from daily thermograph records.

	3 inches	9 inches	18 inches
Minimum.....	55.4	59.0	56.3
Mean minimum.....	59.9	62.6	57.9
Maximum.....	93.2	68.0	59.4
Mean maximum.....	80.6	64.4	58.1
Mean.....	69.8	64.4	57.9

leaf litter persists in the upper quarter of D, nor in E, F, or G, due to wind action and fewer plants. This bare upper part of the transect has only a 42 percent slope in contrast to the main part below it which has a uniform 58 percent slope. Aspen reproduction thins out abruptly at the same elevation, and no aspen whatever occurs in F and G. The lowest *Gilia haydeni* occurs at the bottom of E. This rosette plant, together with *Cirsium megacephalum* and *Lupinus* sp., are the only herbs in F and G; they are so scattered that the ash is essentially bare.

The ash at the summit of Flagpole Cone at 8,308 feet supports only a few individuals of the annuals *Gilia haydeni* and *Phacelia intermedia*, flowering early in August, and a lone wind-trained *Pinus edulis* at the very peak. The latter tree is 33 inches high but is evidently of considerable age. The needles on the lee side are of the ordinary adult type, but on the windward south side the exposed foliage is peculiar in having many tufts of juvenile leaves such as are found on young seedlings of this species. A white bulb anemometer left near this tree, with its bulb 14 inches above the ash surface, averaged 89.5 ml daily water loss from July 1-3, and 62.6 ml daily from August 2-27. The evaporation rate surpasses those found elsewhere, because the rising warmed air from within the crater sweeps across the summit. Unit G at the south end of the belt transect includes the peak but most of this square, beyond the peak, is at the top of the long cinder slope into the crater. There the fine red-brown ash lies at its angle of repose on the 67 percent slope: due to its south exposure, porosity, and instability it completely lacks any visible plant life.

LAVA SINK-HOLE PONDS

In the lowest, northern lobe of the Grants Bed within the Apache-plume belt, are found permanent ponds in tube cavern sink-holes. They range from shaft-like pits, two feet across, to open ponds more than an acre in area. In the narrow portion of the San Jose valley between McCartv's and the western boundary of the Acoma Reservation 105 such ponds were counted. Many of these occur in the area included within Figure 9, but are not clearly visible from this distance and low angle. Several open ponds occur in the lava near San Raphael, but none were found anywhere farther south in the lava bed. Since the recent basalt flows of North America occurred in arid regions, permanent ponds in lava beds are unreported elsewhere on the continent. Discussion of the very cold pools overlying ice will be postponed to the section on ice caves.

Nichols has published several geological studies of the last six miles of the flow, within which all the known ponds occur. He stated (1939) that the gradient of this portion is about 30 feet per mile and that, where narrow, the lava is probably as much as 50 feet thick, with 30 feet as an average thickness.

The water supplying the ponds and the subsurface reservoir, which is in equilibrium with them, drains

from the Zuni Mountain watershed, largely beneath the lava which occupies the valley. Large springs at Horace, one half mile above the ponds, flow uniformly throughout the year at the rate of 5 second-feet (Hodges 1938) indicating that they are fed by a large reservoir. They empty into the Rio San Jose. Its present channel is silted up and relatively impervious so that, although in the vicinity of the sink-hole ponds the stream water level stands four to five feet above that in the ponds, very little water escapes to the lava in this part of its course. The old channel, north of the lava and along the base of the hill, still holds standing water in places, at a level very similar to the water table in the lava. This indicates that the water reservoir in the lava feeds the old channel, and the finding of a bubbling spring at the north edge of the lava tongue bears this out.

The water level in the ponds fluctuates considerably. The weather station at Acomita airport, three and one-half miles from the center of the pond area, recorded only 0.8 inch precipitation in the six months January-June, 1944. Pond levels at the beginning of July were down within one inch of the minima recorded for them over the subsequent three-year period. Then, during three consecutive days starting July 18, occurred a fall of 2.08 inches of rain. Water-level measurements made July 22 showed a 20-inch rise as a result of the three wet days. Despite another 0.8 inch of rain on July 23-24, the next pond measurements July 28 showed a drop of 10 inches in the water table in the lava bed since the record peak of July 22. Normal annual precipitation at Acomita is 10 inches.

The 24 ponds measured are found within 4,000 feet along the valley, and on both sides of the meridian of the Indian village called Anzac. The water level of the highest or western end of the series, was 6,263 feet above mean sea level in December. The lowest or easternmost pond included is seven feet lower. The water-level records from these 24 ponds were taken on 30 dates scattered from July 1, 1944 to July 6, 1947. Plotting the 24 curves showed that adjacent ponds parallel each other very closely in their fluctuations. However, the fourteen ponds in the western 1,000 feet fluctuate considerably more than the ten farther down the valley, and are much more responsive to precipitation. In the ponds of the eastern 3,000 feet of the series, there was only a nine-inch difference between the highest and lowest levels during the four years, in contrast to the 30 inches of the western ponds. This damping effect may be due to the greater breadth of the flow there, or to less pervious deep channels through the lava in this part.

Table 11 presents a quantitative analysis of the water in Horace Spring and in three of the lava pools in order of increasing distance from the spring, or from west to east, over a distance of one mile. The spring is slightly more alkaline than the ponds which harbor plant life. A general decrease in solute concentration is evident as the distance from the spring increases. This can be explained for most

TABLE 11. Analysis of spring water from beneath Tertiary lava, and of selected lava bed ponds near Anzac, August, 1946. Solutes in p.p.m.

	Springs at Horace	Pond 2	Pond 8	Pond 15	Pond 16
pH	8.5	7	8	8	8
Total solids	1388	1313	1150	863	885
Sulfates as SO ₃	485	439	402	269	286
Calcium oxide, CaO	260	216	198	173	166
Magnesium oxide, MgO	134	110	106	74	49
Phosphate, PO ₄	0	0	0	0	0
Total carbonates as CaCO ₃	29	29	22	18	22
Bicarbonates HCO ₃	24.4	35.4	22	16	22
Carbonates, CO ₃	5.3	0	2.7	2.7	2.7
Nitrates, NO ₃	0.42	0.35	0.34	0.40	0.33
Oxygen consumed from per- manganate	2.3	5.3	2.4	2.1	2.3

items by the increasing degree of binding of these solutes in organic form by plants and animals as the water seeps eastward from pond to pond. No phosphate was detected in any of the samples.

Sixty-five pH determinations by comparator block and color ampoules showed the pH of pools ranged from 7.1 to 8.4. The sub-lava water reservoir in the depths of unlighted pits ranged from 7.5 to 8.1.

The 475 water temperature readings, including surface and bottom temperatures, were taken largely in 1944-45. A distinct difference prevails between the pits, with openings less than 12 feet in diameter, and the open sinkholes where the opening measures more than 12 feet across and a large area surrounding it may have subsided to form a sloping approach (Fig. 16). The narrowest pit was a cylindrical shaft about two feet in diameter, which dropped 13 feet to the water table, and continued ten feet below the water. Differences in exposure to sun and wind, and the residual heat of the lava in winter, bring about marked temperature differences between these two habitats. Table 12 gives average surface and average bottom temperatures by months for the five pit ponds, and for 20 of the pools in open sinks. The latter show mean monthly surface temperatures higher than those of the bottom in all months, with greater surface-bottom differences in summer. On the other hand, the pit ponds show a temperature inversion, having the surface warmer than the bottom in summer but colder in winter. The constancy of water temperatures in the pit ponds is striking. The bottoms varied only about 7° F between the highest (July) and lowest (January) means. Their monthly mean surface temperatures ranged through only 12° F.

The surfaces of the pit ponds rarely if ever freeze, while many of the open ponds form ice as much as an inch in thickness. This ice was centrally located in the pond, usually surrounded by a ring of open water about 16 inches wide between the ice edge and

TABLE 12. Monthly mean water temperatures (°F) of lava bed ponds.

	Jan.	Feb.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
In Sheltered pits										
Surface	46.6	46.6	50.9	54.5	59.0	58.1	56.1	52.0	50.2	
Bottom	48.7	47.8	48.6	50.9	54.7	56.7	55.2	51.8	51.1	
In open sinks										
Surface	45.0	45.5	57.6	60.6	65.1	66.0	59.5	56.5	45.7	
Bottom	44.4	44.2	50.9	55.2	59.9	60.4	58.1	54.3	44.1	

the lava rock of the pool's rim. This contrasts with non-lava ponds which start freezing from the edges. The massive lava around the pool holds over heat from the warm season, or absorbs energy from the winter sun, warming the adjacent water enough to prevent the surface water, even though in contact with the cold air of winter, from freezing. In those ponds with gently sloping rock edges, this effect is less pronounced or absent.

The residual heat of the lava mass has another effect on winter temperatures in the more sheltered of the open ponds. The water temperature immediately beneath the ice is, of course, 0° C. But the bottom water at a depth of only 2.5 feet directly below, which theoretically should not exceed 4° C (the point of water's maximum density), may be as warm as 6° C. A temperature range of 6° C is unusual in such a short vertical distance, but more significant is the impossibility of a normal winter period of stagnation even when ice-covered. Convection currents must keep the water in circulation under the ice, as the water warmed at the bottom rises, then, when it becomes cooled again to 4° C nearer the ice, sinks back.

Many of the sink-hole ponds are well protected by the overhanging surface lava, since only a portion of the tube cavern's roof collapsed to form the entrance. In extreme cases the opening may be only a couple of feet in diameter. Within, the pit may broaden out to a diameter of forty feet. The water generally lies 12 or 13 feet below the lava flow surface. In all such ponds, the unicellular green alga *Chlorella vulgaris* Beyerinck forms a thin floating film even in extremely dim light. As reported previously (Lindsey 1949b), a peculiar golden reflection phenomenon is conspicuous from the line of incident light, but disappears completely when the observer steps laterally beyond a certain angle, the magnitude of which depends on the diameter of the cave entrance. This glow of reflected light (Fig. 15) is a consequence of the optical effect in which the refraction of light passing through the spherical cell wall concentrates the dim light on the chloroplast, which maintains an orientation on the cell wall opposite the cave entrance. In well-illuminated water, neither the orientation nor the reflection occurs. The *Chlorella vulgaris* bloom floating in very dimly lighted pools with bare rock bottoms corresponds with the open water stage of ordinary aquatic succession, since low light intensity retards further progress, although this condition is practically permanent and



FIG. 15. In cave ponds *Chlorella vulgaris* surface bloom shows a peculiar optical effect, a unidirectional yellow glow seen best to the left of the dark exposed water surface.

the poor illumination is not due to the depth of water over the bottom. The pool may be very shallow, but is too dimly lighted for the next stage, the algal crust, to appear on the bottom rocks.

The age of all these ponds is essentially the same, since the lava crust subsides into the hollow tubes occurred when the flow cooled. Therefore, the various stages of plant succession which have been reached by the ponds depend chiefly on the original depths of the ponds rather than differences in age.

ROCK-CRUST ALGAL COMMUNITY

In the deeper ponds, or others where soft ooze has not obscured the uppermost submerged boulders, the lava which is permanently submerged supports a dense crust of blue-green algae. The incrustation, which is not slippery to the touch but firm like the surface of morocco leather, averages approximately one-half inch in thickness. It is easily pulled away from the rock substrate because of a white crumbly layer of marl next to the lava, which bubbles furiously when touched with a drop of dilute hydrochloric acid. The blue-green algae constituting the crust vary in presence and proportions, and include *Calothrix parietina* Born. & Flah., *Amphithrix janthina* Born. & Flah., *Phormidium incrustatum* Gom. and *Entophysalis cornuana* Sauvag.

Several unusual features characterize the myxophycal crust. The algal trichomes are vertically oriented, their erect growth producing a grossly visible palisade arrangement. This determines the clean vertical fracture of the brittle crust. There is also, at right angles to the vertical trichomes, a differentiation into growth layers paralleling the substrate. These layers of increment are readily seen wherever the structure is well preserved, both in the recent green part and in the upper part of the white portion farther down. As many as 27 double layers are revealed by a dissecting microscope. Green color is conspicuous in only the uppermost six annual layers, which are also thicker. The green layers average 0.9 mm in thickness, while those below become compacted to one third as much. Below the lowest or

oldest discernable layer, the white calcium carbonate is crumbly and granular.

The differentiation into horizontal layers is brought about by two alternating bands seen when the crust is broken or sectioned vertically. The narrower of these has a salmon color, is smoother and more compact, and is lustrous in appearance. This is the highly calcified layer; it is built up when growth is slow in early spring and possibly in winter. In May the narrow, calcareous, slow-grown layer is still the uppermost one. The alternating wider layers are lighter in color, less dense, and less calcified. The growth of the crust seems to be confined to the surface layer for the most part, the crystals of calcium carbonate probably shutting off much of the light from the deeper layers.

In spite of the marked lime-depositing ability of these Myxophyceae, no heavy deposits of solid marl, such as would indicate lime formation during any considerable geological time span, were seen. This tends to corroborate other evidence relating to the recent origin of this lava flow.

This is the earliest successional stage found in ponds where there is sufficient light for any visible plant life except *Chlorella vulgaris*. Progress to the next stage is extremely slow, and no pit pond has gone beyond the myxophycal crust stage. There is little organic material produced which could fill in the spaces between the rocks, leaving this process largely to wind-carried materials. *Lemna minor*, which occurs profusely in many of the open ponds, was never found in the pits. Its absence indicates that passage of water through the lava body from pond to pond is not by way of open cracks at or near the water table.

OOZE COMMUNITY

The biota of organic ooze deposits and the open water over it (Fig. 16) represents the next successional stage. In most ponds where this is predominant, the soft flocculent bottom is dull olive green and includes diatoms of the genera *Cymbella*, *Amphora*, *Navicula*, and *Synedra* as well as non-filamentous green algae. Half an inch beneath the colored surface the muck is black. It is extremely fine textured throughout. No vascular aquatics are found at this stage. *Lemna minor* may be abundant on the surface from this on through the reed-marsh stage.

One pond, 60 feet in diameter and 2.5 feet deep, is consistently brighter than any other at all seasons. Most of the year it is a vivid emerald green over the entire bottom. When this obtains, over the muck surface practically a pure growth of *Scenedesmus bujuga* (Turp.) Lagerh. is found. During June and July, when this alga is least dominant over the diatoms the color of the bottom is olive green. Although this unusual pond lay only 30 feet from (and had a sub-lava water connection with) another pond very rich in red sulfur bacteria and filamentous green algae, neither of these were ever found in it, despite the fact that quantitative analyses showed the waters of the two are practically identical chemically.



FIG. 16. Small sinkhole pond with fine muck bottom being invaded from the edge by *Scirpus validus*. The light floating mass at the left is *Lemna minor*.

A strikingly disjunct distribution is found in a rare epizooic plant characteristic of the green ooze pond and a few others of this stage. In the water, particularly within a few inches of the pool's lava bank, is a profusion of the actively swimming copepod *Scapholeberis mucronata* (Müller). This crustacean is normally transparent and slightly brownish, but here it is a conspicuous green color, because its carapace is covered by a dense aggregation of the stalked euglenoid *Colacium calvum* Stein. This organism has been reported very few times from North America, and only from Wisconsin, Ohio, and Lake Erie. None of the other genera of copepods supported this commensal.

Loose dark mats of blue-green algae rest upon the non-green organic sediment of some ponds at two or three feet depth. The species constituting these are *Oscillatoria chalybea* Gom., *O. formosa* Gom., *O. chlorina* Gom., *O. tenuis* Gom., *O. amphibia* Gom., *Spirulina major* Gom., *Phormidium tenue* Gom., and *Coelosphaerium collinsii* Dr. & Daily. Occasionally such masses break free and spread upon the pond's surface as dark green rafts of tenuous incoherent material.

In still another type of ooze community, the black muck is covered by a dense concentration of the macroscopic cell masses of the red sulfur bacterium *Lamprocystis roseo-persicina* (Kütz) Schrot. As a result, these pond bottoms appear conspicuously rosy or violet in color. The odor of hydrogen sulfide is often detectable from the water of ponds that harbor this organism. The analysis of the water in the pond with the best growth of this microbe is shown in Table 11, under "pond 16."

This pond was much lower in magnesium oxide

than any of the four others sampled, and slightly lower in calcium oxide and nitrates. Only one of the other ponds had a lower sulfate concentration. *Lamprocystis* occurred in some of the ponds of the western or terminal portion of the lava lobe in the narrow valley; none was found in the eastern half of the pond area. In the latter the water shows a considerably higher total solute concentration and is especially rich in sulfates.

Late in the season many ponds representing this stage support a profuse growth of *Lemna minor*. The decayed remains of this plant, in the absence of any bulkier vegetation, is important in depositing soft, black muck and thereby in fostering successional advance. The surface of this fine muck lies from two to four feet below the pond surface. Except for the upper foot, the deposit has become fairly firm, so that in the dry season when the water is shallow one can walk across these pond bottoms with hip boots, over deep muck. Probing with an iron rod failed to reach the bottom rock and showed that the muck was at least six feet deep in several ponds, including that shown in Figure 16. The original height of an uncollapsed tube in this part of the lava bed averages about 20 feet, but only seven or eight feet of this is below the water table, and where the roofs subsided they furnished rocks that make the pond shallower.

Blank microscope slides left suspended in the surface water for one week were found to be covered with a conspicuous film made up largely of the bacterium *Lamprocystis*; also present were some filaments of the blue-green alga *Plectonema nostocorum* Gom. and a few very young *Stigeoclonium tenue* (Ag.) Kütz. Various slides left for two and three

weeks showed the latter alga dominant in the opaque green deposit of attached plants, and some *Oscillatoria chalybea* Gom., *Oedogonium* sp., and many diatoms. The nature of the attached community on these slides varied considerably among different ponds, even though the slides were all left submerged on the same date.

Ponds representing the late stage of the ooze community develop a profusion of filamentous green algae, including many species of *Spirogyra*, *Mougeotia*, and *Zygnema*.

SUBMERGED AQUATICS

The pioneer plant of the larger submerged aquatics is the stonewort *Chara contraria* A. Br. Where well developed this large alga, anchored in the muck, grows erect to form dense mats which may cover the entire pond bottom in an unbroken expanse. In summer the compact crowns often break the lowered water surface. In several ponds a striking appearance results from the color contrast between the deep green alga and the bright violet-rose *Lamprocystis*-covered muck exposed by large openings in the *Chara* mat.

Along the edges of the *Chara* mat near the banks *Potamogeton pectinatus* is found. The only other submerged vascular aquatic seen in any of the ponds was *Rorippa nasturtium*, and this infrequently. The very light, loose consistency of the muck would seem to discourage rooted submerged aquatics.

REED MARSH STAGE

Scirpus validus generally initiates the reed marsh stage; it is shown invading the open water of a small pond in Figure 16. *Typha latifolia* plays a very similar ecological role except that it does not here invade quite such deep water as does bulrush. The two species occur in mixture in the well-developed reed marsh stage (Fig. 17). Their rhizomes grow in the muck or among rocks and do not form floating mats.



FIG. 17. A typical circular reed-marsh sinkhole with in the Apache-plume (background) belt along the Rio San Jose.

The water parsnip *Berula erecta* often forms a lower stratum beneath the dominant species; it may be rooted in the muck or else its rank compound leaves are buoyed up by the aerenchymous floating root system. Although *Berula* is never the first emergent aquatic to appear in a pond, it often ex-

tends as a broad floating mat from the edges of the cattail-bulrush cover over water too deep for the latter.

Several of the smaller collapse-depressions have water about two feet deep in the center where the roof fell in, with a dense growth of *Scirpus*, while between this and the pond's edge is a circular moat of deeper water which has remained in the blue-green algal rock-crust stage.

Common in the reed-marsh stage, but of less ecological importance, are *Scirpus olneyi*, and *Scirpus paludosus*.

Some ponds have been shoaled chiefly by a long period of deposition of the debris from cattail and bulrush vegetation, whereas those along the south edge of the lava tongue owe their advanced successional stage largely to silt washed into them from outside the lava area. In either case, reed (*Phragmites communis*) has come in and dominates the reed-marsh. Some sinks one-half acre in extent are filled from bank to bank with this species. It is also characteristic along the outer border of the cattail zone, farthest from the central open water of less advanced ponds. In depressions which harbor some reed but are becoming too dry for it, occur *Distichlis stricta*, *Juncus balticus*, and *Asclepias subverticillata*. Still drier parts of these same depressions are invaded by *Hordeum jubatum* and *Muhlenbergia asperifolia*.

A few ponds contain water during the rainy season only, and harbor typical temporary pond fauna and vegetation. *Polygonum longistylum* var. *omissum*, *Rumex mexicanus*, and *Eleocharis calva* cover much of the bottom.

The most advanced successional stage found in former pond sites is the shrubby community made up of *Salix exigua* and *Forestiera neomexicana*. This occurs in sinks that contain standing water only for brief periods during the rainy season.

ICE CAVES

At higher altitudes of the Grants Lava are approximately ten ice caves. The lava tubes there near the sources of the lava are much larger and much farther underground than the tubes in the pond area. A geological description of ice caves in general was presented by Henderson (1933). The most accessible of those in the Grants Lava is maintained as a tourist attraction at the Ice Caves Resort. It was one of the caves used by Harrington (1934) as a basis for his explanation of the occurrence of ice in lava tube caves. This hypothesis requires that the cave entrance open to the south, allowing the low midday sun of winter to strike well into the cave and warm the rocks there. The resulting rising current of warmer air is said to induce a circulation which draws in cold surface air through cracks farther back, thus forming and maintaining the ice. In summer, the higher sun fails to penetrate far into the entrance, so that the heavy cold air remains static over the ice. While the explanation may fit caves of this description, there are three ice caves in this region which are deep, rather open pits completely

closed at the bottom where in summer a pool of icewater overlies the ice; the two with the most ice have their slanting openings facing directly north (Fig. 18). Their ice is about 80 feet below the flow's surface. Two of these clearly show a solid unfissured rock wall behind the ice; one of the two has the floor of the entrance solidly filled in with soil. There could not be any significant circulation of air in either direction through the plugged bottom of the pit to or from the deeper portion of the tube beyond. The other has an old but quite distinct high-water mark on the rock wall 121 inches above the present ice level, showing there is no fissure there capable of furnishing a circulation of air. In these cases Harrington's explanation cannot apply; it seems probable that the ice-bodies originate from direct rainfall, seepage water, and especially the drifting snows of winter collecting in the impervious depths of the pits. The surface thaws to form a summer ice-water pool as much as fourteen inches deep, but the coldest air from the lava surface in winter drains down to the pit bottom. There it remains stagnant due to its greater density and the lack of convection. During the warmer months it remains chilled by yielding the heat which is absorbed by the gradually melting ice. The high water mark in "Lichen Cave" and the recession of ice in the public Ice Cave, point to a current warm-dry climatic trend.



FIG. 18. North-facing entrance of a very open ice cave, where the first North American specimens of the "arctic-alpine" moss *Homomallium incrustatum* were collected.

That the wind-blown surface snow of winter contributes a large amount of the moisture which becomes ice is evidenced by an analysis of the icewater. This is remarkably pure, containing, in one of the caves, only 30 p.p.m. of total solids, which includes only 16 p.p.m. of mineral or fixed residue. There are no sulfates, combined oxides, hydroxide, nor carbonates; a mere trace of calcium and magnesium occurs. The water has a lower solute concentration than is often found in distilled water in the laboratory. The direct catch of summer rain by the pits is doubtless also significant because of their funnel-like form, although the annual precipitation there is only about 15 inches.

In the main cave at the Ice Caves Resort (Lee

1926) which is open to the public, a flat floor of clean ice of unknown thickness covers that two-thirds of the main room nearest the entrance. Farther back, a vertical to overhanging semicircular wall of ice nine feet high borders the higher ice mass which is insulated above by a cap of rock debris that fell from the cave's ceiling. Lee's description of the ice cliff as 14 feet high in 1926, and his photograph, make it clear that a striking recession and lowering has taken place since then. Growing directly on the exposed face of the ice wall, so densely that a general green color is imparted to the surface, are cells of the myxophycous algae *Stichococcus subtilis* (Kütz.) Klerck. and *S. bacillaris* Nag. Many of these plants are living where the maximum light reaching them never exceeds five foot-candles, and the air of that part of the cavern never showed a temperature above 32° F. It is evident that this high ice mass was once continuous across the room, since the wall shows clear differentiation into perfectly horizontal layers marked by clear firm ice alternating with thinner layers of white porous ice, representing periodic increments during the time of ice upbuilding. An attempt was made to fit measurements of these bands to the known tree-ring record for this general area of the Southwest, but the 43 years of exposed ice layers provided too short a sequence. There is a distinct banded arrangement visible in the surface film of blue-green algae, because their cells cover the ice more thickly on the less dense, whiter ice layers, where the surface is slightly more irregular.

The flat ice floor in front of the wall is for the most part much better lighted, and around its front edges becomes slushy, or even covered by a thin layer of water over small areas in midsummer. Here on perpetually solid ice, as well as in more limited melting spots, is an extensive emerald colored growth of the green alga *Sphaerella lacustris* (Girod.) Witt. It occurs in places where the midday light is as little as 20 or as much as 320 foot-candles, but the temperature is never higher in its immediate environment than that of melting ice.

The first report of green cryoscopic algae from North America was made by Kol (1941) from the Yellowstone. None of the three ice algae from the lava caves were among the seven green snow-algae found by Kol. Her world survey of reports of green snow reveals that *Stichococcus* has been found but once before growing cryoscopically; this was in Antarctica in 1908. More species of green snow algae have been identified from Antarctica than from other continents; however, the present writer spent 13 months at Little America in the Bay of Whales region without seeing or hearing of any. There seems to be no previous record of *Sphaerella lacustris* growing on ice or snow anywhere.

One of the ice-water ponds is in a deep pit opening northward; the crescent-shaped pool is exposed to full northern sky light. In some years ice remains exposed all summer (Fig. 19), in others its upper part melts and the water surface is completely covered by a dense floating green bloom of *Sticho-*

coccus bacillaris and *Sphaerella lacustris*. Both are abundant also in debris resting on the ice at the pond bottom. The former alga and some diatoms were the only autophytes growing on the submerged ice in a much more sheltered pit where the light intensity never measures more than 30 foot-candles. In another such pool which was slightly better lighted, *Schizogonium murale* Kütz. occurs.



FIG. 19. Lichen Cave's ice-water pool (black), covered with *Stichococcus-Sphaerella* bloom, surrounds crescentic ice mass. The cave floor, from pool upward, has a lower xeric lichen belt, moist moss belt (dark band), and upper xeric lichen belt.

In three ice pits, the lava rock beyond and above the ice-water pool is covered by a pure stand of *Protococcus viridis* Ag., from the high water line to a distance of four feet above it.

The diversity of habitats in the Grants flow, and the uniqueness of some of these, has led to the occurrence of a number of species, in both the flora and fauna, representing disjunct distribution. Biogeographically the most interesting is the "arctic-alpine" moss *Homomallium incurvatum* (Schrader) Loeske. It has heretofore been doubtful that this species occurs in North America. Grout (1932) wrote, "I have been unable to find an American specimen." The moss was collected in 1948 from the northeast-facing wall of the ice cave just north of the tourist cave at the Ice Cave Resort. The cave is identifiable by the crescentic pool, well exposed to north light. The vegetation on the lava surface about this ice cave station is dominated by Douglas fir and ponderosa pine. The altitude is about 7,800 feet, which is much too low alone to provide "arctic-alpine" conditions as far south as New Mexico. This seems to be the first case on record in which climatic compensation is furnished an arctic-alpine plant in the south by an ice cave habitat or any situation other than very high altitude.

Neither *Pohlia wahlenbergii* (Web. & Mohr.) Andrews nor *Tortella tortuosa* (L. Turn.) Limpr. seem to have been reported from New Mexico previously (Bartram 1931). They were collected from the ice caves. Of the 28 species of mosses collected from the outspread lava area, nearly all are meso-

phytes from protected sites such as ice caves or crevices in the higher, moister part of the lava bed. More typically southwestern are the few xerophytic mosses of the Apache-plume belt.

ZONATION IN ICE CAVE ENTRANCES

A pronounced zonation of plants occurs in several of the ice caves, from the ice level up to the surface of the lava flow. The pattern is quite different in two caves which open toward the north; one is well lighted to the ice which receives unobstructed light from the sky, while the other's ice receives very diffuse light of only 30 foot candles at most. The former cave (Fig. 18, 19) will be described first.

Growing profusely above a recent high water line is the yellow lichen *Acarospora evoluta* H. Magn. A maximum thermometer left at the bottom of this lichen belt, five feet above the ice, from Aug. 11 to 30, 1948, showed a mean maximum temperature of 45° F for these days. The extreme high was only 45.5, reached on one day. The upper lichen community is dominated by the conspicuous orange *Gasparrinia elegans* var. *brachyloba* Zahlbr. This extends up the cave floor on the large loose boulders to 16 feet vertically above the ice. In the upper several feet it is mixed with the moss *Brachythecium collinum* (Schleich.) Bry. Eur. The *Gasparrinia-Brachythecium* belt between five and sixteen feet is more xeric than the belt next above it because the former receives no direct rainfall. The edge of the overhanging cavern lip 40 feet above is directly over the boundary between these plant communities; rain in the windless pit falls straight down on the moist moss belt, the water trickling through the loose boulders instead of moistening the lichens on the broken surface of the talus-like slope farther down.

Readings were made on the same 14 days between August 11 and 30, from an outdoor-indoor thermometer on the rain line. Its bulb was buried one-half inch beneath the surface of the Hypnum mat, while its other bulb remained in air one foot above the moss-covered rocks, but shaded by a boulder from sky-light. The temperature within the moss averaged 40.8° F, ranging from 37.9° to 46.0°. The air bulb, read at the same times, showed temperatures averaging 44.2°, with a range from 42.1° to 48.0°.

The dominant species of the mesic moss belt between 16 and 31 feet is *Hypnum revolutum* (Mitt.) Lindb. Also abundantly found are *Mnium arizonicum* Aman and *Paraleucobryum nerve* (Thed.) Loeske, while by no means uncommon are *P. longifolium* (Hedw.) Loeske, *Drepanocladus uncinatus* (Hedw.) Warnst., *Ceratodon purpureus* (Hedw.) Brid., *Dicranum rhabdocarpum* Sull. and *Hypnum cunressiforme* Hedw.

A thermometer one-half inch beneath the surface of a moss mat of *Dicranum*, near the top of this belt and far enough up the slope to receive occasional direct sun, average 42.6° F, and ranged from 38.5° to 49.1°. This station is 28 feet above the ice surface.

Thirty-one feet from the ice, vertically, are found the lowest shrubs of the *Physocarpus opulifolius* belt. The 14 temperatures one foot above the ground at this point averaged 55.2° F, with a range from 43.5° to 67.1°. The ninebark extends up to the lava surface 30 feet higher, where a sparse stand of Douglas fir is found on the flat lava. Air temperatures outside the cave, taken at the same times as the cave readings which have been discussed, averaged 74.8° and ranged from 65.8° to 82°.

The other ice cave shows a most striking zonation of communities. It occurs in a depressed basin 270 feet in diameter on the north slope of the first volcanic crater east-southeast of Flagpole Cone. The ice lies about 90 feet below the lava surface of the bowl-like depression directly above, and is much better sheltered from light and evaporation than the cave described first. It occurs in an older (probably Tertiary) flow than is represented by the narrow stream of rough black lava which overrode it in the small valley just north; the pumice-like soil on the surface about this ice cave is very similar to that on Cinder Hill, and a good stand of ponderosa pine occurs. *Juniperus pachyphloea* is found on the sink's edge, while the more mesic *J. scopulorum* reaches large size in the upper part of the depression.

The greater age of this flow has allowed the accumulation of a much deeper soil mantle in this ice cave than in any other. Counting the upper coniferous vegetation as one community, nine distinct zones or communities occur from the ice outward. Air, soil, and water temperatures and atmometric data were collected on 22 visits from June 28 through August 30, 1948, largely at the lines bounding adjacent communities.

The ice, which is of unknown depth, is submerged beneath an ice-water pool which in summer averages about 7 inches in depth. A thin dark debris resting on the ice, at 32° F, when examined quickly under a microscope showed active diatoms, rotifers, and at least three species of protozoans swimming rapidly.

The lowest terrestrial community is occupied almost exclusively by a grossly conspicuous stand of protonemal threads of the moss *Pohlia cruda* (Hedw.) Lindb. These massed aerial protonema densely cover and obscure the lava rock fragments, resembling a layer of green velvet about one-eighth inch in thickness. The protonemal belt is about four feet across the narrowed cave floor. In its upper third are found widely scattered and inconspicuous sterile erect gametophytes of the same species only; this makes identification of the protonema possible. In this definite though small community, the protonemal stage has reversed roles with the erect later stage and is here, curiously, the long lived, propagative and dominant phase of the life cycle. It tolerates the inhibiting effect of constant cold much better than the erect plant of the same species, under conditions which exclude the many other species which occur elsewhere in the same cavern. A thermometer was left near the lower edge of this belt, among the protonemal threads at their level, and read eleven times during July and August. It indicated an

average temperature of 34.1° F, with a range from 33.3° to 34.9°. *Pohlia cruda* is a common and widely distributed moss, found from the far north to the tropics; its toleration of a wide temperature range, as well as the constant cold of this ice cave, is noteworthy. It would be most interesting to learn whether at the northern limit of its world range the protonema behave in the same way as in this ice cave.

The next higher community forms a band across the cave, approximately seven feet wide in the direction of the cave's axis. It is dominated by the erect stage of the same species, and includes some *Tortella tortuosa*.

Behind and above the ice water pool, the coldest part of the vertical rock wall is greened over with *Protococcus viridis*. Above this, and about three feet above the pool, in the dimmest light found in any moss habitat, is a profuse growth of the very fine-textured moss *Amblystegiella sprucei* (Bruch) Loeske. A maximum thermometer kept in this moss colony during August, never went above 1.6° C.

Comparisons of light intensities were made with a Weston Sight-light Meter, which is rather accurate at low intensities since it covers the range of only 0.75 foot-candles. On an overcast day, August 24, when an ordinary Weston exposure meter pointed at the open sky read just 1,000 foot-candles, no part of the *Amblystegiella*-*Protococcus* community received more than one foot candle, and much of the *Protococcus* considerably less. The maximum light received by the ice water pool at any point was 30 foot candles. Readings toward the entrance at the level of the *Pohlia* protonema averaged 40, while the maximum light in this protonemal belt, all along its upper edge beyond which erect sprouts are abundant, was 135.

Conditions found on a bright August noon-day, when bright sunlight from clear skies to the south was reflected into the cave from a white cloudbank in the northern sky, represent the absolute maximum of light available for photosynthesis in this cave. The brightest point on the pool was still receiving only 35 foot-candles, the moss-*Protococcus* received 8 at most, while the protonema farthest from the entrance received only 14.

Returning to the cavern floor, the belt above the *Pohlia*-*Tortella* community shows a mixture of *Brachythecium collinum* (Schleich.) Bry. Eur., and *Pohlia wahlenbergii* (W. & M.) Andrews. The boundary line between these adjacent belts showed an average daytime temperature from June 28 to August 30 of 35.1° F.

At the upper boundary of this *Brachythecium* belt a pair of white and black bulb atmometers was set up together. Very little evaporation took place. The white bulb averaged 2.0 ml daily loss from July 29 to August 30, 1948, while the adjacent black bulb lost a 2.3 ml daily average.

Next above the *Brachythecium* belt occurs the most varied plant community of the cave entrance. The most conspicuous plant is *Marchantia polymorpha* L. Much of the liverwort occurs on a sloping

surface receiving the light from the entrance at a low angle. Only female conceptacles have been seen on any of the plants in this large colony. Their stalks (gametophytic) are evidently more strongly phototropic than negatively geotropic, and as a result point rather directly toward the brightest entrance light. The stalks on the steepest part of the slope are practically prostrate on the thalli.

Other bryophytes found commonly in this rich community are *Drepanocladus uncinatus*, which is the dominant outside of the Marchantia areas, *Ceratodon purpureus*, *Hypnum revolutum*, *Dicranum rhabdocarpum* Sull. Two thermometers were left through the summer in different places along the boundary between this uppermost bryophyte community and the one below, with their bulbs buried at the soil surface not more than one-half inch beneath the plant mat. The 42 readings averaged 41.9° F.

At the upper limit of the Marchantia belt it meets the sharply bounded *Ribes inerme* shrub growth. The dense *Ribes* stand extends about 25 feet horizontally along the cave's axis, and seven feet vertically. Its lower limit would seem to be determined by the low soil temperature, which averages 33.1° F at nine inches. The shrubs do not go under the sink's south overhang where direct light from the sky would be cut off. The soil in the *Ribes* zone has been built up so that it covers all but the largest lava boulders; it is deep, fine-textured and quite black because of its high organic content.

Several feet from the upper edge of this community a white-black atmometer pair was maintained during the same month as the lower pair. The level of the bulbs was 15 inches, so that they were about half as high as the plants and surrounded by them. The black sphere lost 32 percent more than the average daily loss of the accompanying white one, whereas at the boundary between the two uppermost bryophyte zones, the reduction in radiant energy resulted in an average loss by the black sphere (22.1 ml) only 15 percent greater than that of its white partner (16.7 ml).

The next higher community is dominated by ninebark. *Physocarpus monogynus*, which extends upward to the conifers or to the base of a sheer rock wall of the sink. The rocks of the entrance slope are larger here, with soil less abundant and largely restricted to spaces between boulders. Direct sun impinges for long hours on this community; it is considerably more xeric than the *Ribes* belt. *Yucca baccata* occurs at its upper limit. *Muhlenbergia arvensis* is prominent.

A white atmometer sphere placed 15 inches above the lava at the top of the ninebark community showed an average daily water loss (corrected) of 37.3 ml.

For control data, white and black bulb atmometers were maintained as a radio-atmometer on the lava surface outside the cave and forty yards lateral to it among the ponderosa pines. From July 6, the black sphere lost water over a 49-day period, at a

rate 15 percent more than the average daily loss from the white sphere, which lost 47.8 ml daily.

OTHER SHELTERED TERRESTRIAL HABITATS

In the Douglas fir belt near the Ice Caves is found a broad circular hole in the lava about sixty feet deep. The northern, larger part of its flat bottom supports only the same gray *Parmelia* lichen vegetation found here on the lava surface. But the southern portion forms a green crescent of deep *Hypnum revolutum* and other mesic moss species, which cannot grow here in habitats receiving much direct sunlight. Just at noon on July 5, the moss distribution corresponds almost exactly with the crescentic shadow of the south wall cast on the floor. At only one place did the edge of this shadow fail to coincide with the limit of moss occurrence. This was where the thin shade of a small juniper growing upon the rim permitted a somewhat sparser moss growth, which however, did not extend at all beyond this partial shade into the sunlit part of the depression's floor.

Where the lava is extremely rough, approximately 1.5 miles down the flow south from the Ice Caves, but nearer its west edge, in the dim light at the bottom of a crevice about 14 feet deep, *Neckera neomexicana* (Card.) Grout was collected in July, 1948. With reference to this moss, E. B. Bartram, who identified it, stated in correspondence, "... so far as I know this is the first time it has been seen since the original collection was made in Socorro County (New Mexico)." In the same site *Pseudoleskea arizonae* Williams, *Orthotrichum anomalum* Hedw., and *Tortula ruralis* (Hedw.) Sm. occurred.

Shelter for lower plants is sometimes provided on the general flow surface by hollow squeeze-ups, which were described geologically by Nichols (1939b). Widely varying light and moisture may be found in these, depending on the location and amount of roof collapse. The best examples exist at the Ice Caves region in the Douglas fir belt. An overarching bubble-like squeeze-up about five feet high, opening to the north, is the only station for the thalloid liverwort *Reboulia hemisphaerica* (L.) Raddi. The moss *Tortula ruralis* (Hedw.) grows there in dim light, together with the lichens *Peltigera canina* (L.) Willd., *Parmelia coloradensis* Gy., *Physcia pulverulenta* (Schreb.) Nyl., and *Anaptychia mexicana* f. *isidiophora* B. de Lesd.

In all three vegetation belts, the small fern *Cheilanthes feei* is anchored in minute joints on vertical north-facing walls of deep crevices and sinks.

The only colony of any mesic fern (Fig. 20) found anywhere in the recent lava area was in the northeast lobe at an altitude of 6,265 feet. There *Asplenium trichomanes* L. was previously reported (Lindsey 1945) to occupy the top of the small central island of a pit pool. The moss *Eurhynchium fallax* (R. & C.) Grout grows beneath the fern. Neither has been reported from elsewhere in the 220 mile lava area or its vicinity.



FIG. 20. *Asplenium trichomanes* occurs only on this site, a roof-rock island surrounded by a pond in a sheltered sub-lava cavern.

A white-black atmometer pair was maintained in this cavern, with the bulbs four inches above the level of the fern fronds, from June 28 to Sept. 1, 1948. During this hottest period of the year, the daily average loss by the white bulb was only 2.6 ml of water, while the black bulb evaporated nearly the same, or 2.5 ml daily.

At noon on June 28, 1948 the sling psychrometer showed a relative humidity of 22 percent on the lava above, while that in the cave over the ferns was 50 percent. A maximum thermometer left among the ferns out of direct sunlight on June 28, indicated 59.9° F on July 31, and 60.4° F on August 28.

From August 29 to Sept. 1 a three-pen recording thermograph was left in the cavern. The bulb lying on the surface lava, outside but on the rim of the entrance, showed a mean temperature of 84.9° F, and extremes of 132.8° F and 51.8° F. The other bulbs were not exposed to direct sunlight. One lying among the low *Asplenium* fronds recorded a mean of 58.5° F and a range from 55.4° to 62.6°. The third bulb, submerged one-half inch beneath the pond's surface, showed a mean of 57.7° F and a range from 57.2° to 59°. The means are based on readings at hourly intervals. The patterns for the different days were closely similar. The uppermost bulb was only eleven feet above the submerged bulb. There is, in sheltered pit-pool caverns in this climatically most xeric lobe of the Grants Bed, a very steep vertical gradient in temperature and vapor pressure deficit, between the interior and the air outside.

SUMMARY

The Grants Lava Bed along the continental divide in west central New Mexico contains 220 square miles of relatively bare, largely Quaternary, lava. The altitudinal range from 8300 to 6200 feet is reflected in three climatic and vegetational belts on the general flow surface. Three weather stations near the highest belt have an average annual precipitation of 13 inches and a mean annual tempera-

ture of 47° F. Precipitation comes in July, August, and September. Three stations near the lowest belt average 10 inches in annual precipitation, and a mean annual temperature of 51°. The upper vegetation belt of mixed Douglas fir and ponderosa pine, the intermediate one of ponderosa pine, and the lower belt of Apache-plume shrub, represent a series of decreasing mesophily.

In the Douglas fir belt, *Juniperus scopulorum* is second to the dominant species in abundance and basal area, but exceeds all other plants in crown cover. In the ponderosa pine belt, no Douglas fir occurs, probably due to lava surface temperatures lethal to its seedlings; shrubby species of *Quercus* and *Rhus* are prominent. Both vegetational belts are postclimax to the adjacent vegetation on non-lava substrates. Climatically, there is more frequent, and probably greater, precipitation induced by convection over the heated black lava. Edaphically, precipitation is more effective in lava because little rainfall is required to raise the water content of the sparse soil in crevices to field capacity. Consequently, ponderosa pine attains commercial importance on the Grants lava under an annual precipitation of 15 inches, although this species requires 20 inches in northern Arizona.

In the Apache-plume belt, *Fallugia paradoxa* covers 2,500 square feet per acre; the second species in importance, *Rhus trilobata*, covers 360 square feet. The dominant shrubs are shallow crevice plants. Rough aa-type lava is bare except for lichens.

Water loss from white-bulb atmometers in the Apache-plume belt exceeded that in the other two belts. Evaporation stress at the Douglas fir station slightly exceeded that in the ponderosa pine belt, because of more wind.

Because soil is usually lacking or sparse and thin in the lava bed and its adjacent terrain, parent materials are highly important in determining plant distribution. Forty-one common species, mostly herbs, are characteristic of only one of the nine main substrate types. Cinder benches show stronger ecological similarity to physiographically young granite substrate than to other volcanic deposits such as cinder cones, lava flows, or lava con's. Of 17 herbs characteristic of cinder cones, 11 were characteristic of no other habitat. On the north slopes of cinder cones, mesic conditions, reflected by a mean daily atmometer loss of only 30 ml for August, permit normal growth and reproduction of Douglas fir in contrast to the dwarfed, atypical form of this species on lava.

The fastest growing ponderosa pines are on cinder benches while those under the same climate that grew most slowly occur on granite. *Juniperus pachyphloea* is rare on lava and common on cinder con's, whereas *Fallugia paradoxa* is restricted to lava. The relation of the various substrates to the water factor is the principal cause of the marked differences in the characteristic plants. Even on the favorable cinder bench habitat, available water was absent at times during the growing season.

Many permanent ponds in depressions resulting

from the collapse of tube caves—an aquatic habitat unique in this continent—occur in the lower, northeast lobe of the flow. The water level fluctuates considerably. The pH of the ponds ranges during the year from 7.1 to 8.4, and the total solids average as much as 1380 p.p.m. The monthly mean bottom temperatures of shallow ponds in confined sinkholes fluctuate only 39° F between July and January. Stored heat in the lava keeps water circulating beneath the ice of exposed ponds in winter.

Successional stages in lava ponds are: (1) floating *Chlorella* bloom, (2) rock-crust blue green algae, (3) organic ooze stage, (4) submerged aquatics, (5) reed-marsh, (6) temporary pond, (7) shrubby swale. No pit ponds have gone beyond the second stage, due to low light intensity.

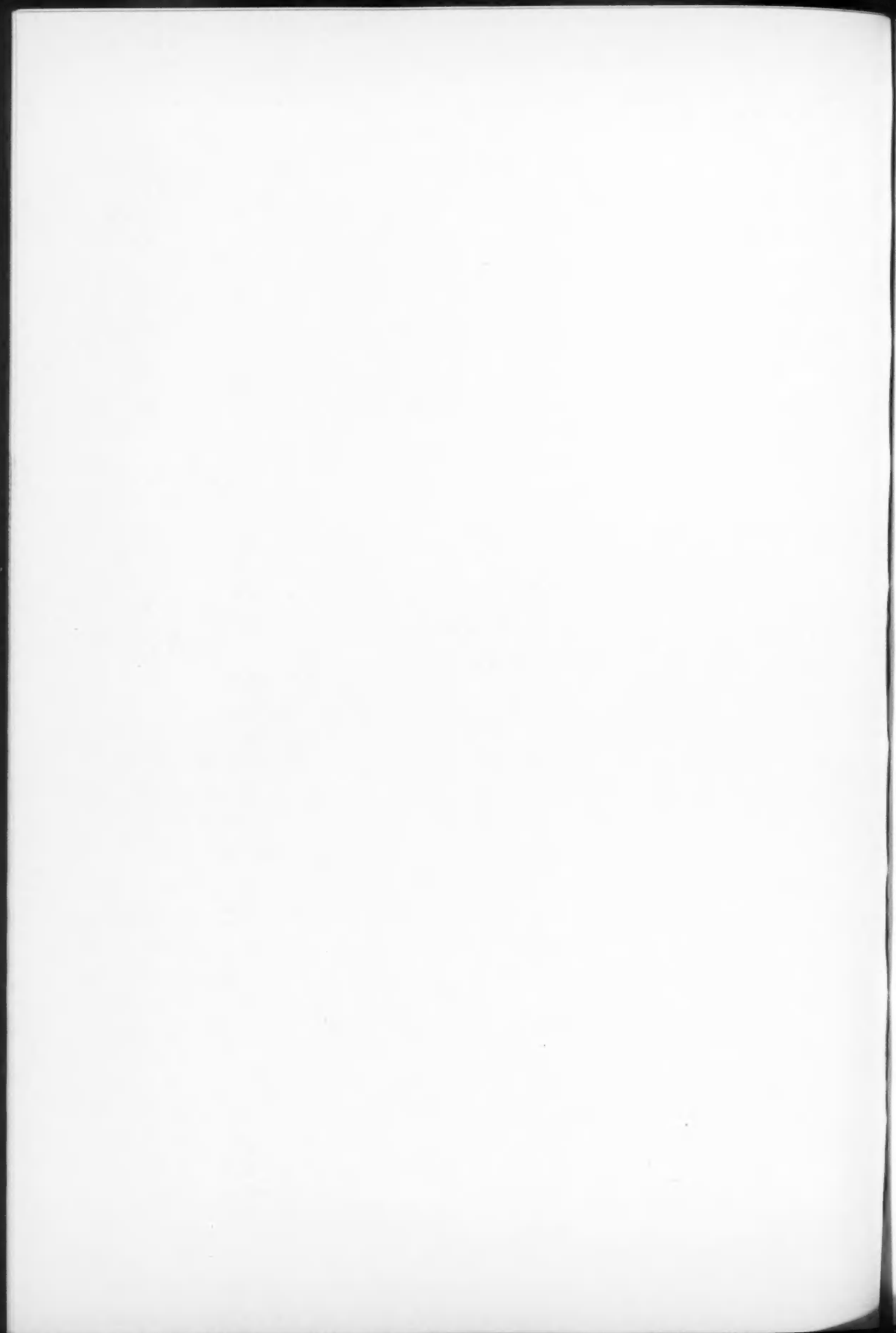
At high altitudes on the flow, permanent ice masses are features of several large tube caves. The blue-green algae *Stichococcus subtilis* and *S. bacillaris*, growing at 32° F where maximum light intensity is as low as 5 foot candles, impart a strong green hue to the ice surface. *Sphaerella lacustris* grows on ice in a range of midday light from 20 to 320 foot candles. None of these plants has been previously reported growing cryoscopically elsewhere than in Antarctica.

The deep entrances of ice caves possess a definite zonation of plant communities. One cave shows 9 zones from the ice-water pool to the ponderosa-pine surface community. Five of the zones are characterized by bryophytes, and the two above these by shrubs. The lower zones have extremely uniform temperature conditions during the growth season.

Other special microclimatic conditions with associated terrestrial plant assemblages occur in collapse depressions with or without some water, deep crevices, hollow lava squeeze-ups, and other sheltered sites. Lichens, mosses and ferns characterize such habitats. A high proportion of cryptogams of widely disjunct distribution occurs in the special habitats of the Grants Lava Bed.

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STUDIES ON PLANT SUCCESSION IN TRUE PRAIRIE

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	255	Relative Productivity of Prairie and Pasture	
LATE STAGE OF SUCCESSION IN AN UNGRAZED		Grasses and Forbs in Subseres and Prairie..	261
NATIVE PASTURE	255	REGENERATION OF NATIVE GRASSES IN A	
History During and Following the Drought.....	256	BLUEGRASS PASTURE	262
Comparison of Developing Vegetation with		History of the Prairie and Pasture.....	262
Climax Prairie in 1948.....	256	Methods	262
Methods	257	Environment and Development of Vegetation	
Relative Distribution of Grasses.....	257	in 1948.....	263
Relative Distribution of Forbs.....	259	Test of Vigor of Big Bluestem.....	264
Changes in 1949.....	259	Survey of Relict Bluestems Outside Exclosures..	264
Little Bluestem Type.....	259	Vegetation within the Exclosures.....	264
Big Bluestem Type.....	260	Environment and Recovery in 1949.....	265
Big Bluestem-Bluegrass Type.....	260	SUMMARY	267
Decrease in Sand Dropseed.....	260	LITERATURE CITED.....	267

INTRODUCTION

Most work on plant succession has been done on the earlier stages only. This is probably because these stages are most obvious and that great changes occur in relatively short periods of time. Conversely, in grasslands, at least, the process of stabilization, as will be shown, is not so obvious nor so rapid. It can be followed only by exact methods of measuring, mapping, and comparing the vegetation year after year during a long period of time. Such studies, for example, have been made in both mixed and true prairie by Weaver & Albertson (1943, 1944) and in true prairie by Weaver & Hansen (1941a), Weaver & Bruner (1945), and Weaver (1950).

The present studies are in the main based on the background of knowledge of previous development of the vegetation or, in some instances, of its degeneration. This previous work makes the present findings more meaningful, even though the period of this study was only two years. The present research includes two separate parts—plant succession following grazing and drought, and plant succession where degeneration of grassland was halted in time for rapid recovery.

The writer wishes to acknowledge his obligations to Dr. J. E. Weaver for outlining the problem and continuous efficient direction during the work. He has also aided greatly in organizing the data.

LATE STAGE OF SUCCESSION IN AN UNGRAZED NATIVE PASTURE

A large tract of unbroken native prairie lies 3 miles north and 1 mile west of the University of



FIG. 1. General view from north to south of the recovering pasture (right) and the adjacent climax prairie (upper left) as it appeared in September 1940. Close study shows the north-sloping hillside, a broad shallow ravine, and the nearly level land in the foreground. The vegetation at this time was composed largely of sand dropseed and side-oats grama. Photo by Weaver.

Nebraska. A considerable portion of it had been fenced and grazed continuously for many years. It had apparently never been greatly overgrazed. In 1932-33 it was studied and described as belonging to the mid-grade type of pasture, which is characterized by about half dominance of little bluestem (*Andropogon scoparius*),¹ big bluestem (*A. furcatus*), and other prairie grasses and half dominance of bluegrass (*Poa pratensis*) (Weaver & Hansen

¹ Nomenclature of the grasses is according to Hitchcock's "Manual of the Grasses of the U. S."; that of other species follows Britton and Brown's "Illustrated Flora," unless other authority is given.

1941b). The cover was practically intact, annual weedy species were few, and only a small amount of the usual perennial pasture weeds occurred. In the spring of 1937, a portion of this pasture which adjoined the annually mowed prairie was separately fenced and thus exclosed to livestock. The experimental tract was 4.5 rods wide and 31 rods long. It extended northward from the top of a low hill down a slope of 2 to 5 percent and included its nearly level but well-drained base (Fig. 1). The topsoil or A horizon of the Sharpsburg silty clay loam is 10 to 12 inches deep on the hilltop and slopes, while the Judson silt loam on the lowland has an A horizon 20 inches thick. Both soil types have fairly deep B horizons (12 to 20 inches). The roots of many prairie grasses extend through both horizons and into the loessal parent material beneath.

HISTORY DURING AND FOLLOWING THE DROUGHT

A brief description of conditions during the drought and the trends of succession after the drought (1941 to 1947) until this study was begun in 1948 seems necessary here for clarity.

Great deterioration of the pasture occurred the first three years of the drought (1934-36). In 1937, according to Weaver & Hansen (1941a), both little bluestem and big bluestem occurred sparingly. Bluegrass remained only in scattered patches ranging from a few square decimeters to a square meter in area. Sand dropseed (*Sporobolus cryptandrus*) varied in occurrence from sparse to abundant as did also side-oats grama (*Bouteloua curtipendula*). Small amounts of blue grama (*Bouteloua gracilis*), June-grass (*Koeleria cristata*), and a few other native grasses were found. Dense patches of *Lepidium densiflorum* occurred throughout much of the pasture and *Plantago purshii* was very abundant in widely distributed patches. These, with *Solidago glaberrima*, *Aster multiflorus*, and *Leptilon canadense*, were the major constituents of the weed flora.

Drought occurred each growing season until 1942; but conditions for growth were favorable in spring and early summer of 1938 and 1941. Drought was definitely broken in 1942, and excellent growth occurred in 1943 and 1944. From extensive studies of permanent quadrats (Weaver & Hansen 1941a, Weaver & Bruner 1945), it has been shown that the invading sand dropseed made a steady increase (94 percent) until near the end of the drought. It continued to gain during the severe drought of 1939-40, when nearly all other grasses decreased. But this was followed by a gradual decrease as the more mesic grasses regained their vigor. Side-oats grama increased even more rapidly than did sand dropseed. The four-year gain was 413 percent. But with the return of good years it also decreased in abundance. The relict little bluestem gained 332 percent by 1940, and even more during the following good years. Kentucky bluegrass had increased only slightly by 1940, but very rapidly in 1942-44.

Only 5 native forbs were of major importance. During the drought years they constituted 90 percent of the total native forb population. Among

these, *Aster multiflorus* and *Solidago glaberrima* increased greatly, then waned, and later were suppressed.

"Near the end of the drought in 1940, sand dropseed dominated in many places. It still grew in mixture with side-oats grama, but over much area with the bluestems as well. It had been locally replaced by bluestems which had greatly thickened their stands. The bunches and mats of other prairie grasses were also both thicker and more vigorous. Bluegrass had made only slight gains. The patches of goldenrod and aster were somewhat thinned by the grasses, and the plants were dwarfed. The annual weed stage of *Plantago purshii* and *Hedera hispida* had nearly disappeared. After 8 years (1937 to 1943 inclusive) and especially three consecutive good years, succession toward the climax was again well under way. Only in a few places was sand dropseed still abundant. The bluestems and side-oats grama dominated except in parts of lowlands where bluegrass formed a dense sod. There was no bare soil. All the weedy annuals had disappeared; aster and goldenrod were also absent or greatly subdued. An understory of various minor prairie grasses, bluegrass, and forbs was rapidly developing. Under the dense stand of prairie grasses there was a good mulch of fallen debris. But the absence of certain species of prairie grasses and forbs, common in the adjacent climax prairie, and the lack of various community relationships indicated that succession was still incomplete." (Weaver & Bruner 1945).

Four years later, in the spring of 1948, the present study of the late stages of this subseries was begun. These years, except for an occasional period of summer drought, were good years, and an approximately normal crop of forage was produced annually. This was removed in the fall at the time the prairie was mowed for hay. Most of the grasses normally attained a general level of 12 to 18 inches by mid-July when vegetative growth was nearly complete.

COMPARISON OF DEVELOPING VEGETATION WITH CLIMAX PRAIRIE IN 1948

A thorough study of the regenerating prairie was made during the summer of 1948. Special attention was given to the composition and structure of this subseries in comparison with that of adjoining climax vegetation. Repeated observations revealed that the developing vegetation was composed of three rather distinct although intergrading communities or types. These corresponded somewhat with topography and type of soil. The steeper portion of the north-facing slope, which included about one-third of the area, was being occupied by the little bluestem type and will be so designated, although actually the matrix of sand dropseed, bluegrass, and side-oats grama was more extensive. The lower slope and the upper, broad, flattened portion of a ravine occupied the middle third of the area. Here there was a transition from the Sharpsburg silty clay loam to the deep Judson silt loam northward on the more level

but also well drained land. This central section was dominated mostly by large bunches of big bluestem alternating with a sod of Kentucky bluegrass. The remaining third of the area was nearly level and entirely on Judson silt loam. It was dominated mostly by the sod type of big bluestem, with much smaller amounts of bluegrass.

METHODS

In addition to very careful, repeated observations, listing of forbs, and the use of list and clip quadrats, large representative areas were mapped. The part mapped for detailed study included portions of both subser and climax prairie. A portable wooden frame 6 feet wide and 12 feet long was used. It was divided into 72 sections, each one square foot in area, by means of heavy cords stretched tightly across the frame. In locating the places to be mapped, a line was run near the middle of the long narrow pasture and a similar parallel line about 60 feet east of it through the western portion of the adjoining prairie. These lines were on opposite sides but parallel with the fence which originally separated the pasture from the prairie. Beginning near the south end, twelve sampling areas were laid out along each of the lines at equal intervals of 12 paces. Only alternate samples along each line were mapped.

In the mapping, each square foot was examined separately and the space occupied by each species,

as bunches of little bluestem, prairie dropseed (*Sporobolus heterolepis*), etc., was accurately shown on the chart (Fig. 2). Areas of big bluestem are indicated by dots. These not only show the presence of this species, but their abundance also indicates something of the density of the stand, but not the number of stems. Vertical lines indicate the presence of sand dropseed and the number of lines something of its density. This scheme, with horizontal lines, also holds for Kentucky bluegrass, as do the check marks for small tufts of side-oats grama. Frequently the last two or three species were intermixed to form a matrix of sod. In this manner were shown the areas occupied by bunches of grass, the relative proportions of the sod-forming grasses, whether pure or intermixed, and the approximate area occupied by each species or mixture.

Mapping the distribution and approximate abundance of all the more important grasses and forbs afforded an excellent means of direct and exact comparison of subser and climax vegetation. The twelve maps, including 432 square feet in the subser and a similar area in prairie, clearly revealed differences between the late stage of the pasture subser and the climax prairie in 1948. Three pairs of the maps are shown in Figures 2, 3, and 4.

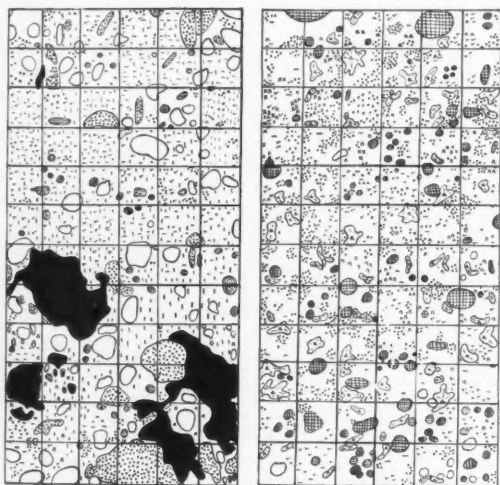


FIG. 2. Maps of the vegetation in pasture (left) and prairie (right) in the little bluestem type. Symbols of the grasses are as follows: blue grama, solid black; little bluestem, enclosed, more or less circular areas; big bluestem, dots or enclosed areas with dots; prairie dropseed, cross hatch; tall dropseed, enclosed circles; needlegrass, enclosed s; Junegrass, enclosed cr.ss; side-oats grama, check marks or enclosed horizontal lines; Kentucky bluegrass, horizontal dashes; and sand dropseed, vertical dashes. Symbols of the forbs are: *Amorpha canescens*, enclosed a with radiating dashes; *Solidago glaberrima*, inverted u; *Artemisia gnaphalodes*, printed g; *Aster multiflorus*, an x; *Helianthus rigidus*, an H, *Kuhnia glutinosa*, a K with radiating dashes.

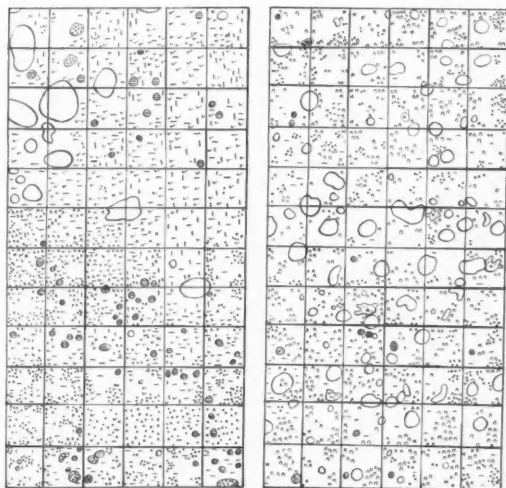


FIG. 3. Maps of the vegetation in pasture (left) and prairie (right) in the big bluestem type. Symbols for species are the same as in Figure 2.

RELATIVE DISTRIBUTION OF GRASSES

Blue grama (areas in black) was absent in the prairie. It was found in the pasture in several small patches on both upland and lowland.

Little bluestem (enclosed, more or less circular, unmarked areas) within the pasture samples was always sparse or absent although it did occur in the south end of the pasture in sufficient abundance to rank as a leading dominant. Except in this little bluestem type, there was always more little bluestem in the prairie adjacent to each of the pasture

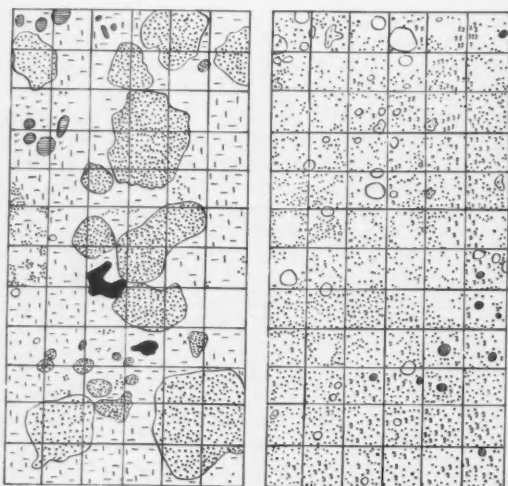


FIG. 4. Maps of the vegetation in pasture (left) and prairie (right) in the big bluestem-bluegrass type. Symbols for species are the same as in Figure 2.

types. As a whole, it was more than three times as abundant in prairie as in pasture.

Big bluestem (dots) in the little bluestem type of pasture grew sparingly and mostly in small bunches, indicating recent establishment. In its own type in the subser, it grew in large bunches (1 to 3 feet in diameter) and sometimes occurred as an interrupted sod. In the big bluestem-bluegrass type, it also occurred as large bunches which were surrounded by a matrix of sand dropseed and Kentucky bluegrass (Fig. 5). In places the bunches had spread and fused to form a dense sod. This was in sharp contrast with conditions in the prairie where bunches seldom were found. In the prairie, it formed a uniform sod of medium to moderate density. There was almost as much big bluestem in the pasture as in prairie.

Sand dropseed (vertical dashes) occurred over the whole pasture area, but it was not found in any part



FIG. 5. Bunches of big bluestem in the pasture on June 21, 1948. They developed from smaller ones that survived the great drought, often in a dormant condition. By 1949 many merged to form a continuous sod. Note the bluegrass in the foreground and between the bunches. This bluegrass sod also contains much sand dropseed. Photo June 21, 1948.

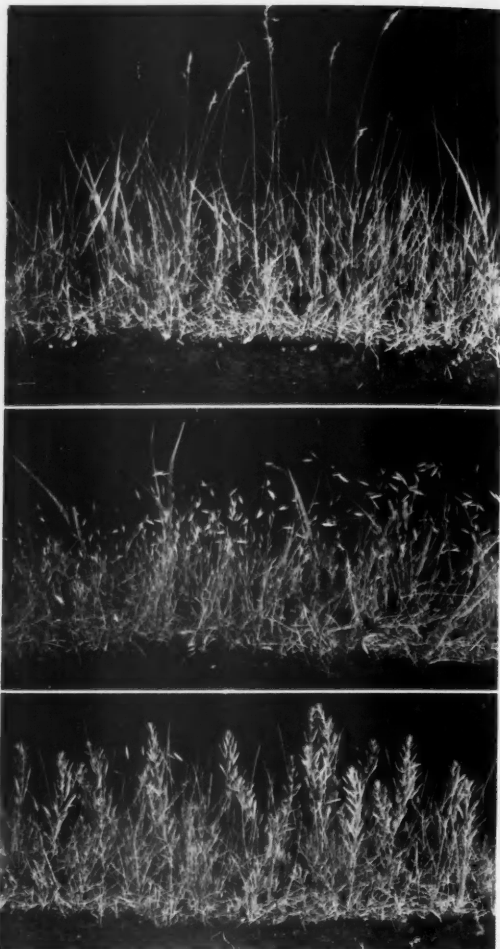


FIG. 6. Detail of three extensive kinds of sod-mats in the little bluestem pasture type. (Upper) Bluegrass-sand dropseed mat with small amounts of side-oats grama. The bluegrass has the finer leaves and is in blossom. (Middle) Sand dropseed with a dense stand of hairy chess. (Lower) Bluegrass sod with a thin stand of *Aster multiflorus*. Average height of the foliage in each picture is about 5 inches. Note the dense stands and good soil mulch. Photo June 15, 1948.

of the climax prairie. This species was often associated with bluegrass and side-oats grama and with them formed large patches (30 to 40 feet or less in width) of a subser matrix which was common in many places in the pasture (Fig. 6).

Kentucky bluegrass (horizontal dashes) was usually sparse but always present in the prairie where it is a long-established invader (Weaver & Fitzpatrick 1934). In the pasture it was quite abundant and scattered widely; the density of the stand varied inversely with that of the mid and tall grasses. There was only about a third as much bluegrass in prairie as in pasture.

Side-oats grama (check marks or enclosed hori-

zontal lines) was often thinly intermixed among the other grasses of the matrix in all the pasture types; rarely was it aggregated into small tufts over three inches in diameter. In the prairie it nearly always occurred in bunches and was never as abundant as in the pasture.

Tall dropseed (*Sporobolus asper*), shown in enclosed circles, was scattered throughout on the upper slope in the prairie but only a few small bunches occurred in the pasture maps. Prairie dropseed was entirely absent in the part surveyed, but was sometimes plentiful on the hilltop in prairie.

Penn sedge (*Carex pennsylvanica*) occurred sparingly and in the higher portion of the prairie only. In the pasture it was likewise largely confined to the upper third or the little bluestem type, but it was found here in greater abundance than in the prairie.

Hairy chess (*Bromus commutatus*) was scattered thinly throughout the whole area dominated by little bluestem in the subere. It was scarcely found elsewhere; none occurred in prairie.

RELATIVE DISTRIBUTION OF FORBS

The prairie was characterized by an abundance and wide distribution of *Amorpha canescens*. In an area 2 rods in width and extending the entire length of the prairie adjoining the pasture, 1,062 plants were found. In a sample area of similar width and length in pasture, only 35 occurred. These were all much smaller and younger plants; the original population of this very palatable legume had probably long ago disappeared under grazing.

The *Helianthus rigidus* formed dense societies in prairie, because of its propagation by rhizomes. Not a single isolated sunflower was found in the pasture. However, three of the societies had slowly extended their size by migrating beyond the old fence-line, in one instance to a distance of 18 feet. The new patches were several yards in width.

The dense societies of *Solidago glaberrima* in the subere (Weaver & Bruner, 1945) had now been reduced by years of competition with the returning grasses. They were not only much less abundant than formerly, but even fewer than in prairie. The weedy *Aster multiflorus* likewise had clearly decreased since the years of drought, but it was still more abundant here than in prairie. The very deeply rooted *Vernonia baldwinii*, as is usual, had increased under pasturing from its former single or few-stalked condition in prairie (Weaver & Fitzpatrick, 1934). It occurred sparingly in the prairie but was common in the subere.

The following native species occurred commonly but not abundantly in both pasture and prairie: *Astragalus crassicaupus* Nutt., *Petalostemon candidum*, *Erigeron ramosus*, and *Kuhnia glutinosa*. The legumes, at least, had migrated in rather recently (cf. Weaver & Hansen 1941a).

Examples of species common in the adjoining prairie but not found in the subere were *Rosa pratincola*, *Glycyrrhiza lepidota*, *Meriolix serrulata*, *Lia-*

tris punctata Hook., and *Echinacea pallida*, but there were many others.

Another group of weedy plants, commonly found in old pastures, were still scattered in the subere but were never seen in the prairie. These were *Trachypogon pratensis*, *Gaura parviflora*, *Asclepias verticillata*, *Acerates lanuginosa*, *Cirsium undulatum*, *Verbena stricta*, *Convolvulus arvensis*, *Euphorbia marginata*, and *Lactuca scariola* L.

Ambrosia psilostachya occurred sparingly in prairie but it was abundant and thriving in many places in all types of the subere. This species migrated eastward from mixed prairie during drought. Other species of forbs were of very minor importance and ecological significance.

CHANGES IN 1949

Profiting by the detailed acquaintance with the area in 1948, careful observations were continued in 1949, but it did not seem necessary to remap the sites. This was a wet year; the precipitation from January to September was 5 inches above the normal 20.44 inches. The soil was wet and the vegetation showed a remarkable development. This was revealed not only by the production of rank foliage and flower stalks but also by the increase in density of stems and by the rapid spreading of certain species.

LITTLE BLUESTEM TYPE

Chief difference in the stabilized prairie was that of greater foliage and flower production. But in the subere remarkable changes occurred as vegetation rapidly approached the climax. Little bluestem increased enormously both in number of tufts and size of bunches. In fact, the foliage height (16 inches) and abundant flower stalks made this species much more prominent here than in prairie. Its actual gains were so great that in many parts of the area it now formed a normal stand (Fig. 7).

Big bluestem likewise had made tremendous gains since the preceding year. It was not as uniformly distributed as little bluestem, but in many places the two-foot foliage was from stems that formed a dense sod extending over several yards. Elsewhere it occurred in smaller patches and bunches but was



FIG. 7. View in the little bluestem type, July 30, 1949, showing a normal abundance of little bluestem. The sod-mat of bluegrass and sand dropseed has greatly decreased.

by no means local. A few scattered bunches of Indian grass (*Sorghastrum nutans*) were thriving.

Sand dropseed was rapidly decreasing. It was dying or absent under the bluestems. Hairy chess was sparse and dwarfed. Side-oats grama was far less abundant than formerly and the plants were stunted. Bluegrass was waning as climax species increased. The former matrix of bluegrass, side-oats grama, and sand dropseed, or any one or two of these, had a greatly decreased area. It was estimated after continued study that this decrease was about 40 percent since 1948. These low-growing grasses, bordered by the much taller bluestems, had the appearance of islands in a sea of taller foliage. This was a marked reversal of the former condition of bunches of mid and tall grasses in a matrix of bluegrass. Forbs were not especially abundant, except the invader, western ragweed. They were all thriving and had gradually increased in numbers; some well established societies occurred.

The understory was indeed poor. Penn sedge had decreased greatly with thickening of the general foliage cover; other low-growing species were few. There was a good soil mulch, not only in this type but also throughout the subere. Air-dry weight of mulch calculated from 10, 5-square-foot samples amounted to half a ton per acre. Moreover, this was approximately equal to the amount found in similar widely separated areas in prairie. The very uneven height of the vegetation as a whole, which characterizes lack of stabilization in true prairie, was still pronounced.

BIG BLUESTEM TYPE

In the big bluestem site on the lower slope and on the broad upper part of a ravine, big bluestem now covered nearly 50 percent of the soil. Intermingled were switchgrass and small amounts of Indian grass. The dominant had increased excessively at the expense of the little bluestem and many other prairie species which shared the soil in the adjoining prairie. Little bluestem composed about 15 percent of the vegetation; the islands of bluegrass and side-oats grama, or an intermixture of these with sand dropseed, made up nearly all of the remaining 35 percent. The general foliage height here scarcely exceeded 12 inches compared with 32 inches for big bluestem. The formerly pronounced bunch-habit of this species was rapidly disappearing as the expanding bunches fused into the sod type. In autumn three levels of vegetation were pronounced: The one of big bluestem (32 inches), that of little bluestem (18 inches), and a lower one of bluegrass and other low-growing species (12 inches).

It would seem almost certain that with continued good years big bluestem would overwhelm other vegetation, but that this does not occur in adjoining prairie would contradict this prediction. In the prairie, big bluestem is not continuous and does not seem to be more than a third as abundant as in this type in the subere. There its dominance is shared by switchgrass, little bluestem, needlegrass, prairie dropseed, and other grasses together with a large

number of well developed societies of forbs. In the subere, prairie forbs were few and societies poorly developed.

BIG BLUESTEM-BLUEGRASS TYPE

Succession seemed less rapid in this portion of the pasture which recovered from drought earlier than the remainder. Fully 90 percent of the increase in prairie dominants was due to the spreading of big bluestem (Fig. 8). Little bluestem spread only slowly in the matrix of bluegrass sod. There was some invasion and spreading of needlegrass. Side-oats grama was decreasing together with sand dropseed, although both were better developed here than elsewhere in the pasture. Drought populations of aster and goldenrod had been largely ousted; ragweed was still plentiful. The cover remained irregular as regards height, the understory was poorly developed, and societies of forbs were rare.



FIG. 8. Abrupt transition to an island of bluegrass, a yard or more in width to dense growth of big bluestem in flower at a height of 5-6 feet. The light colored plant in the bluegrass (foreground) is *Artemisia gnaphalodes*.

DECREASE IN SAND DROPSEED

Since sand dropseed was so very abundant in the early stages of the subere, special studies were made on its behavior. These quantitative data are based on 10 permanent quadrats, each a square meter in area, which had been located at random throughout the pasture in places where this species was abundant. Population of sand dropseed, stated in hundreds of stems in the 10 square meters, during the dry years of 1937 to 1940 were 62, 74, 90, and 121, respectively (Weaver & Hansen 1941a). Thus, the number was almost doubled during this period when the climax grasses of prairies were greatly reduced in numbers. During the years of good rainfall, 1941 to 1943, the total number of stems decreased year by year to 105, 69, and finally to 61 hundred, a total decrease of 42 percent during the three years (Weaver & Bruner 1945).

In 1948, the writer ascertained by further counts that a decrease of 65 percent in the 1943 population had occurred leaving only 21 hundred stems. The fact that sand dropseed was yielding slowly and that

relict plants were common even in a dense mat of bluegrass or other low-growing species is shown by the persistence of dwarfed individuals even in 1948 in more than half (532) of the square decimeter areas (Fig. 9). A final count in 1949 revealed only 700 stems, a decrease of 67 percent from the preceding year. The total decrease was 94 percent from the time the sand dropseed population was highest (12,100 stems) at the end of the drought to its present low ebb of 700 in 1949.

RELATIVE PRODUCTIVITY OF PRAIRIE AND PASTURE GRASSES AND FORBS IN SUBSERE AND PRAIRIE

Little is known about the relationship between total yield of grassland and its stage of development toward the climax. When the yield of climax prairie grasses is considered separately from that of subsere (pasture grasses) some interesting relationships appear. It has been found in this experimental area that the yields of prairie grasses in the dry year of 1940 increased uniformly from the part of the pasture protected the first year, a second year, and a fourth year, respectively, to climax prairie. The yield of pasture grasses however, had an entirely different sequence. "Prairie grasses, as listed below, included all plants of grasslike habit that were found more or less regularly in normal, undisturbed prairie. Pasture grasses included similar species not common to climax eastern Nebraska prairies, and bluegrass which is a long established invader." (Weaver & Hansen 1941a.) This does not mean that prairie grasses do not occur in pastures. In fact, in good native pastures they furnish the great bulk of the forage. The division into prairie grasses and pasture grasses is merely one for convenience.

PRAIRIE GRASSES	PASTURE GRASSES
<i>Andropogon furcatus</i>	<i>Aristida oligantha</i>
<i>A. scoparius</i>	<i>Cyperus filiculmis</i> (a sedge)
<i>Bouteloua curtipendula</i>	<i>Eragrostis cilianensis</i>
<i>B. gracilis</i>	<i>E. pectinacea</i>
<i>B. hirsuta</i>	<i>Hordeum pusillum</i>
<i>Carex pennsylvanica</i>	<i>H. jubatum</i>
<i>Koeleria cristata</i>	<i>Poa pratensis</i>
<i>Panicum scribnerianum</i>	<i>Sporobolus cryptandrus</i>
<i>P. virgatum</i>	
<i>Sorghastrum nutans</i>	
<i>Sporobolus asper</i>	
<i>S. neterolepis</i>	
<i>Stipa spartea</i>	

The annual yields of prairie grasses in the subsere, recorded in percentages, based on the prairie as 100 percent and beginning with the first year of protection, were 8, 18, 67, and 100. Thus, on the weight-basis the successional trend is clearly indicated. The annual yield of pasture grasses based upon the pasture under the first year of protection as 100 percent, were 100, 125, 57, and 5, respectively. This shows a marked increase during the second year, but a great decrease the next. In the climax, pasture grasses constituted 5 percent; most of this was bluegrass. The preceding data are based upon the weights of four clippings of 30 quadrats in each area during the summer of 1940 (Weaver & Hansen 1941a).

In the present studies, the plants were clipped from 20 sampling areas, each containing 5 square

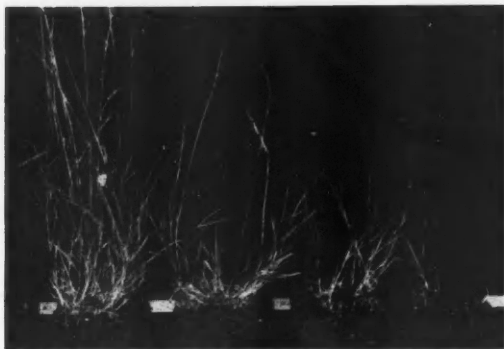


FIG. 9. Four plants of sand dropseed showing stages in degeneration due to competition with climax blue-stem grasses. The vigorous plant on the left was from an adjacent, more open area where it developed in a normal manner. The other three from the subsere, show responses to increased amounts of competition, especially shading.

feet. The harvest was taken about August 15, after the vegetative growth was practically complete. The sampling areas were located at random, seven paces apart, along the lines on which the maps were located in both subsere and prairie. Prairie grasses, pasture grasses, and forbs were clipped, air-dried, and weighed separately in both 1948 and 1949. The average weights for the two years is shown in Table 1.

TABLE 1. Average air-dry weight in tons per acre of vegetation clipped in 1948 and 1949, and percentage increase or decrease.

Kind of vegetation	Subsere wt. tons	Percent total	Climax prairie wt. tons	Percent total	Percent increase or decrease in prairie
Prairie grasses	1.19	77	1.48	78	24
Pasture grasses20	13	.08	4	-60
Forbs15	10	.33	18	120
Total	1.54	100	1.89	100	23

These data show clearly that the bulk of the subsere vegetation (77%) was composed of prairie grasses. Bluegrass and other pasture grasses furnished only 13 percent by weight, and forbs only 10 percent. In climax prairie the percentage of prairie grasses by weight was only slightly higher (78%), but that of pasture grasses, as would be expected, was much lower (4%). The greater amount of forbs in the prairie (18%) is in agreement with data from the maps and general observation.

Comparison of the data on former yield with current production shows that the increment of prairie grasses in the subsere increased from 67 percent of total vegetation in 1940 to 77 percent in 1949. Likewise the pasture grasses which composed 41 percent of the pasture yield in 1940 (Weaver & Hansen 1941a), now furnished only 13 percent. These data also indicate that the subsere was much closer to the

climax as regards kinds and amounts of vegetation than it was 9 years earlier.

REGENERATION OF NATIVE GRASSES IN A BLUEGRASS PASTURE

This study is on successional trends in a once excellent lowland pasture formerly dominated by bluestems. Heavy overstocking from early spring until late fall (about April 15 to October 20) had caused this high-grade pasture to degenerate into a low-grade type in a period of only 4 years. During these years Weaver and Darland (1948) in their research on this 50-acre area gave major attention to the changes in the vegetation resulting from the seasonal grazing patterns of the cattle and how they were affected by environment. The kinds and amounts of forage produced and forage consumption were ascertained month by month and year by year, from 1943 to 1946 inclusive, by means of numerous portable exclosures. The usual heavy rate of stocking, about 45 head of year-old steers or approximately 200 animal-months of grazing, continued in 1947. To understand fully the trends in recovery, when exclosures were installed in 1948-49, a brief history of the rate and degree of degeneration seems necessary. This is taken from their publication.

HISTORY OF THE PRAIRIE AND PASTURE

The pasture occupied a nearly level tract of well drained lowland about three miles northeast of Havelock, a suburb of Lincoln, Nebraska. The dark colored, porous and highly productive soil is Wabash silt loam. In it the roots of big bluestem and western wheat grass extended in thick masses to depths of 6 to 7 feet, and even Kentucky bluegrass penetrated to 3 feet. The original prairie was composed mostly of big bluestem and little bluestem but also of patches of switchgrass and slough grass (*Spartina pectinata*). During the great drought, which began in 1934, the grasses were considerably damaged by desiccation and by burial under deposits of wind-blown dust from surrounding cultivated fields. This resulted in changes of the composition of the vegetation. As a result this prairie, which formerly had been mowed each fall for its large yield of excellent hay, was grazed regularly after 1934.

Four years later (1938) the pasture was composed of three distinct types or communities of plants. Western wheat grass, (hereafter called wheat grass), covered the deeply dusted areas and a few other places where the bluestems had been killed by drought. Kentucky bluegrass formed communities where somewhat more than half and often nearly all of the vegetation was composed of bluegrass. Since this grass was rarely found intermingling with wheat grass, origin of the type resulted from bluegrass more or less completely replacing the native prairie grass. Its type occurred mostly in ravines and adjacent lands where nearly pure stands of big bluestem had been "grazed out." Like the wheat grass community, it occupied approximately one-third of the total pasture area. The remainder was composed of good stands of native prairie grasses

and forbs practically free of invading weeds. This is the only type of vegetation in which regeneration was studied. The other types need no further consideration here except that the low palatability of wheat grass and the relatively low yield of bluegrass (with its decreased palatability when dry) were chief factors in causing a tremendous grazing pressure on the third of the pasture where the bluestem type prevailed. Moreover, the early grazing each year, which started before or shortly after the bluestems had appeared above ground, was very harmful to most prairie grasses.

The bluestems as a type disappeared in 1945; they had been destroyed by overuse. Only weakened remnants of prairie grasses remained in the invading bluegrass sod. By 1946 prairie grass became rare, relict shoots of big bluestem persisting longest. Loss of practically all prairie forbs occurred with the disappearance of the prairie type. In the weakened and less dense bluegrass sod, native weedy forbs and shrubs spread rapidly and many weeds found only in old pastures became established. This foreshadowed the final weed stage in degeneration. In 1947 deterioration continued; the weed population increased in both species and abundance.

METHODS

Several methods were used in this study. In addition to permanent exclosures, in which list and clip quadrats were used extensively, a survey of relict grasses outside the exclosures was made, and also tests of vigor of certain grasses. In April, 1948, locations for two exclosures were selected in the deteriorated pasture just described. It presented an excellent subsere stage which it was believed, would develop to more or less of a climax condition if it were completely protected. One, the west exclosure, was located in the northwestern part of the pasture where big bluestem, needlegrass, and little bluestem were formerly abundant (Fig. 10). The second or east exclosure was located on slightly lower ground in the east-central part of the pasture where big bluestem was formerly more abundant (Fig. 11).

Each exclosure was 48 feet long and 18 feet wide. The fence consisted of a single strip of heavy woven



FIG. 10. Former type of vegetation in the autumn of 1943, where the west exclosure was located in the spring of 1948. The half-grazed bunches are mostly tall dropseed and little bluestem, but needle grass and big bluestem were also plentiful. Photo by Weaver, September, 1943.



FIG. 11. Degeneration of prairie to bluegrass in the eastern part of the pasture. This occurred mostly since 1942. Bunches of various grasses remain, but chiefly tall dropseed, little bluestem, and needlegrass in the sod of big bluestem and bluegrass. The east enclosure was located in this area in 1948. Photo by Weaver, September, 1943.

wire with a mesh 5 inches wide so that it had no visible effect upon the vegetation as regards shading. The woven wire was 26 inches high and was placed at a height of 14 inches above the soil. Two tightly stretched barbed wires, at 6 and 11 inches in height, respectively, prevented the cattle from reaching under the fence, while two similar wires, one 6 and one 12 inches above the woven wire, prevented their reaching over the fence. Sturdy, well-braced posts held the wires securely, hence, the entire enclosure could be used experimentally (Fig. 12). To prevent the blowing in of snow or the congregating of rodents, the vegetation was clipped at 2 inches in height and removed from the enclosure late in the fall. Throughout two years, 1948-1949, development of vegetation in the enclosures was studied in relation to the conditions outside. Pasturing continued during these years at about the same rate and over the same long period of time as in previous years.



FIG. 12. The east enclosure on August 13, 1948. The recovering vegetation within has made only a moderate development due to its weakened condition. The bluegrass outside has been closely grazed.

ENVIRONMENT AND DEVELOPMENT OF VEGETATION IN 1948

The spring of 1948 was late. In April, early growth of the vegetation was interrupted by insufficient moisture. There was no rain during the first two-thirds of the month. Rainfall for April, May, and June, respectively, was .58, 1.00, and 1.02 inches below the normal which is about 4 inches for each

of these months. Thereafter precipitation was in excess of the normal and good growth occurred. By mid-April the bluegrass in the best parts of the sod was 2 to 3 inches high, but in many places it was only 1 to 1.5 inches tall. The winter annuals, little barley and hairy chess, and wheat grass were about the same height.

Vegetation in the east enclosure on April 24 consisted of a continuous sod of bluegrass, except for a few small patches of Penn sedge. This was the part of the pasture which had been in bluegrass for the longest time. A very few weakened stems of needlegrass were found but no bluestems. Forbs were few. Only a single patch of *Antennaria campestris* and a few plants of *Vernonia baldwinii* and *Taraxacum officinale* occurred. The west enclosure likewise seemed to be well sodded with bluegrass. Although the cover was not so dense, the bluegrass was more vigorous. Here the grass was 3 to 5 inches tall. Bunches of needlegrass were common but small. Several species of coarse sedges were also present and small numbers of a half-dozen species of prairie forbs were found. The bluestems, if present, had not appeared above ground. Conditions outside the enclosures, of course, were approximately the same, since grazing had just begun.

An examination of the pasture in mid-June revealed that grazing was, as usual, very close everywhere. Big bluestem was sparse and little bluestem was even less abundant. After an extended search sods containing ungrazed little bluestem were obtained. The tufts of bluestem were small and completely surrounded by bluegrass. This was clipped to the soil surface. These fragments of little bluestem together with ungrazed, vigorous plants from an adjacent prairie are shown in Figure 13. The late appearance of the bluestems which normally renew growth about April 15, was due largely to their weakened condition. The latter had been brought about during past years by too early, too frequent, and too close grazing.

The condition of needlegrass at this time was not

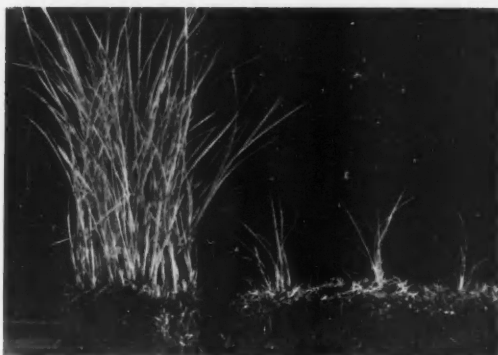


FIG. 13. Relict, weakened tufts of little bluestem (right) from which the surrounding bluegrass has been removed. These late appearing plants are only 4 inches high and although not yet grazed they are greatly dwarfed compared with the normal development of this grass in prairie (left). Photo June 10.

greatly unlike that of the bluestems. Under the lodged bluegrass and weeds of the preceding season some bunches of needlegrass had been protected from grazing. These plants were now past blooming. But mostly they had been weakened so greatly by grazing in former years that they had few stems left and produced no flowers.

TEST OF VIGOR OF BIG BLUESTEM

A test was made of the vigor of the best big bluestem plants growing in the west exclosure with similar ones from a part of the pasture that had been protected two full years. The method used was that described by Weaver and Darland (1947). The blocks of big bluestem were each 10 by 10 inches in size and were taken in May to a depth of 4 inches. In both lots, the grass was 6 inches tall, but this new growth was cut back so that only 2 inches of stubble remained. The sods were transplanted, each into a metal-lined box 10 by 10 inches inside width and 24 inches deep. The boxes had previously been filled with a good loam soil of optimum water content. The sods were placed firmly upon the soil. Water was applied sparingly as needed from time to time. After 5 weeks, one side was removed from the boxes



FIG. 14. Blocks of sod of big bluestem five weeks after they were taken from the pasture and transplanted. (Left) Sod from an exclosure where it had been protected only one month, and (right) from an exclosure where it had been ungrazed for two full years. Differences in development of new roots and tops reflect the greater vigor under protection.

and the soil beneath the blocks of sod was gently washed from the roots. The old sods with the new growth of roots and tops were then photographed (Fig. 14). The weight of tops of the open stand on the recently protected block of sod was only about one-third that produced by the sod which had been protected two years. The more vigorous plants had produced 99 roots with an average length of 18 inches. There were less than half as many roots (46) on the non-vigorous ones. These averaged 14 inches in length. As regards dry weight, roots of the more vigorous plants weighed 16.8 grams, those of the weaker plants only 4.6.

SURVEY OF RELICT BLUESTEMS OUTSIDE EXCLOSURES

A survey of the pasture was made in mid-June to determine the abundance of the dwarfed tufts of bluestems. This survey included about 15 acres in the part of the pasture near the east exclosure which had been in bluegrass for the longest time. Fifteen acres of the part more recently invaded by bluegrass and adjacent to the west exclosure was also sampled. The survey was made along 3 lines in each area. These were about 100 feet apart. Along these lines, a hoop, enclosing one square foot, was placed at random, and the number of stems of the two species of bluestems within it were counted. Two hundred samples were taken. A total of 377 stems of big bluestem was found near the east exclosure, but 668 near the west one. Similar figures for little bluestem were 38 and 105. Moreover, big bluestem was found in only 50 and 73 percent of the samples, respectively; little bluestem was sparse, occurring in only 7 and 14 percent. The fact that bluestems were formerly widely distributed in the pasture is indicated by the occurrence of the relicts in 73 percent of the areas sampled.

The palatability of these species was also clearly illustrated by this survey. Approximately 90 percent of all the stems counted had been grazed in 1948. Many were eaten back to a height of 2 inches or less. Some belated, weakened stems had only recently appeared and were 1 to 2.5 inches tall. They had escaped grazing. Despite this, there were still enough bluestems left to form a nucleus for the re-establishment of a good pasture if they were given adequate protection.

VEGETATION WITHIN THE EXCLOSURES

In the exclosures, dried inflorescences of bluegrass formed a distinct and uniform upper story at a height of 13 inches by mid-June. The green foliage beneath presented an understory 4 to 5 inches high. Only a few spikes of wheat grass and Junegrass extended above the bluegrass in the east exclosure, and a very little wheat grass and needlegrass in the west one. These scattered clumps of needlegrass were dwarfed. Stems varied from 2 to 20 per bunch and ranged from 6 to 14 inches in height. Only occasionally were there flower stalks. Despite its decreased vigor and consequent late appearance, big bluestem now varied in height from 3 to 12 inches.

It was scattered widely in both exclosures. Competition with the bluegrass was severe during the dry spring. Little bluestem was very sparse, the number of stems varied from 2 to 12 per tuft. Sedges and Scribner's panic grass occurred in small patches. A few forbs including *Psoralea argophylla* and *Amorpha canescens* were present. A few plants of ironweed were 2 to 3 feet high; otherwise forbs were not abundant.

To determine the trend in regeneration of the relict prairie species under complete protection, a survey of all species except bluegrass and sedges was made in each square foot of each exclosure in the middle of June. This was done by marking out the entire exclosure into square-foot areas. Heavy cords were fastened to the bottom wire at intervals of one foot. Permanent file marks were made on the wire and painted so that the marks could be used in future study. Counts of all stems of the relict species and the invading sand dropseed were recorded for the 864 square feet in each exclosure. The number of stems of each species and the percent of the total number of unit areas in which each species occurred were ascertained. These results will be compared with the findings in 1949.

ENVIRONMENT AND RECOVERY IN 1949

This second year was one very favorable for an excellent development of vegetation. Temperatures were about normal in spring and the soil was moist. Rainfall in May and June was nearly 5 inches in excess of the normal 8 inches. Excellent weather continued during July and plant production was high despite moderate drought in August. Outside the exclosures there was a good growth of bluegrass, regardless of the usual heavy grazing. A survey was made in the pasture of the occurrence and amount of the relict bluestems. As before, these data were obtained in mid-June (Table 2).

TABLE 2. Number of stems and percent occurrence in 200 square-foot sampling areas in portions of the pasture adjacent to the exclosures.

Site	BIG BLUESTEM				LITTLE BLUESTEM			
	Number of stems		Percent occurrence		Number of stems		Percent occurrence	
	1948	1949	1948	1949	1948	1949	1948	1949
Eastern part.....	377	401	50	50	38	78	7	9
Western part.....	668	475	73	59	105	154	14	12
Average.....	523	438	62	55	72	116	11	11

The excellent environment is reflected in an increase in the number of stems of little bluestem in both sites. Big bluestem increased slightly in one site and decreased greatly in another. The percentage of samples in which the grasses occurred decreased, remained the same, or increased but slightly. Hence any increase in number of stems may be attributed not to new plants but to better growth of the old ones due to the extra protection from graz-

ing afforded by the unusual development of bluegrass, especially the flower stalks.

The survey in the exclosures was also made as before in mid-June. The results of this survey are compared with those of the preceding year in Table 3

TABLE 3. Total number of stems of grasses, except bluegrass, in the exclosures in mid-June of 1948 and 1949. The percentage of the 864 units in which they occurred is also shown, if this amounted to 1 percent.

Species	NUMBER OF STEMS		Percent increase or decrease	PERCENT OCCURRENCE	
	1948	1949		1948	1949
	East Exclosure				
Big bluestem	7,132	44,344	522	79	79
Little bluestem	618	5,009	710	1	1
Needlegrass	640	1,570	145	17	23
Scribner's panic	2,983	7,665	119	77	87
June grass	103	281	172	..	1
Tall dropseed	115	100	-13	1	..
Sand dropseed	2,901	1,283	-52	39	20
	West Exclosure ^a				
Big bluestem	4,333	17,649	307	42	47
Little bluestem	94	995	948	1	1
Needlegrass	2,206	4,510	104	39	45
Scribner's panic	2,033	4,460	119	68	75
Junegrass	19	12	-37
Tall dropseed	218	364	67	3	4
Sand dropseed	102	7	93

which shows clearly that big bluestem was by far the most abundant species. Its stems had increased 307 and 522 percent, or an average of more than fourfold. That only a small part of this was due to the excellent conditions for growth is shown by the fact that outside the exclosures the decrease was 16 percent. Average number of stems per square foot in the exclosures was now 36 compared with 4 outside. The percent occurrence remained constant or increased slightly in the exclosures; in the pasture it decreased 11 percent. The vigor of this species was indicated by the production of many flower stalks of normal width and height (Fig. 15). There were only 28 flower stalks by mid-August of the preceding year as compared with the present 742 stalks. Little bluestem, which was sparse in 1948,

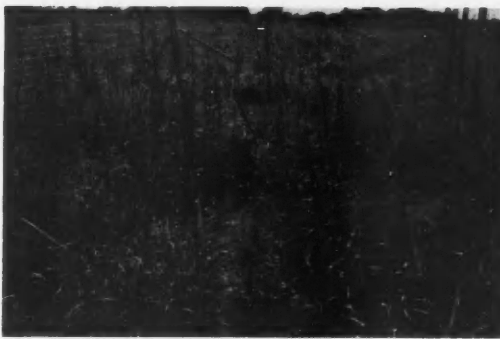


FIG. 15. Portion of the east exclosure on September 8, 1949, showing the excellent development of big bluestem. Some flower stalks were over 5 feet tall.

showed a remarkable increase in number of stems. Even outside the exclosures the increase during this good year, and consequent decreased grazing pressure, was 61 percent. Within the exclosures the increase was eightfold and ninefold, respectively, or an average of 829 percent. The average number of stems per square foot inside and outside the exclosures was now 3.5 and 1.1. Since little bluestem is a bunch grass and the increase was nearly all due to the growth of the established bunches, percent occurrence remained the same. That the plants still were low in vigor was shown by the narrow leaves and small number and size of flower stalks.

Needlegrass within the exclosures made an average increase in stems of 125 percent. It also spread into several new unit areas. Flower stalks were produced in great abundance and the seed crop was heavy. In September, it formed a dense cover and many bunches had attained large size.

Scribner's panic grass was originally widely distributed in both exclosures and represented by two to three thousand stems in each. By the second year vigorous plants were found in many new unit areas and the total increase in stems was 119 percent. Junegrass and tall dropseed were of very minor importance. Sand dropseed, aside from bluegrass, was the only pasture grass of any importance. It was abundant only in the east exclosure, and decreased under the dense cover of foliage, as in the preceding study area. The loss was 72 percent and it occurred in only half the unit areas in which it was formerly found. Accompanying this marked development of the cover a prairie grasses, there was a corresponding decrease in bluegrass.

Only 8 species of forbs occurred. All were rare except *Lithospermum linearifolium*, with a maximum of 90 stems, which was decreasing. The tall, coarse pasture weed, *Vernonia baldwinii*, increased from about 200 stems to nearly 300 in one exclosure; smaller numbers but a similar increase was noted in the other.

The scarcity of all weeds in the exclosures was in marked contrast to their development in the bluegrass sod outside. Here the extensive patches of ironweed, whether the plants were standing or broken off by the cattle and lying on the ground, greatly reduced the stand and consumption of bluegrass. *Symphoricarpos occidentalis* continued to spread widely. *Leptilon canadense* formed dense thickets and greatly shaded the bluegrass. Thistles (*Cirsium undulatum*, *C. flodmani*) wild hemp (*Cannabis sativa*), and numerous other weedy forbs and grasses indicated still further degeneration. In sharp contrast was the increasing regeneration of prairie grasses within the exclosures.

As a final measure of recovery the percentage of prairie grasses, pasture grasses and forbs were ascertained as in the preceding study. This involved, of course, harvesting the forage each year. Eight plots, each 3 by 3 feet in size and located at random

TABLE 4. Yield in grams of prairie and pasture grasses and forbs, and the percentage of total yield furnished by each.

	1948		1949		Percent increase
	Weight	Percent of total	Weight	Percent of total	
East Exclosure					
Prairie grasses.....	790	58	2,310	79	192
Pasture grasses.....	527	38	562	19	7
Forbs.....	55	4	55	2	0
Total	1,372	100	2,927	100	113
West Exclosure					
Prairie grasses.....	511	34	1,615	59	216
Pasture grasses.....	846	57	1,033	37	22
Forbs.....	135	9	121	4	10
Total	1,492	100	2,769	100	84
Average of Exclosures					
Prairie grasses.....	650	46	1,962	69	204
Pasture grasses.....	686	48	797	28	15
Forbs.....	95	6	88	3	5
Total	1,431	100	2,847	100	99

throughout each exclosure, were staked and clipped in mid-August of the first year and the same plots were clipped at the same time in 1949 (Table 4).

Total yield of forage increased greatly, as was anticipated. The amount of increase was 84 percent in the west exclosure, where the previous survey showed big bluestem was less abundant, and 113 percent in the east exclosure. While a part of this increase was a direct result of a better environment, the greater cause was undoubtedly due to increased vigor of the protected vegetation. Near the end of the first year of protection, the pasture grasses (mostly bluegrass) furnished nearly half (48%) of the total average yield of both exclosures. After two seasons of protection they produced only 28 percent of the total. Their actual yield increased only 15 percent in 1949, while total yield of forage practically doubled (99% increase).

Prairie grasses at the first harvest produced an average of 46 percent of the total yield, or slightly less than the pasture grasses. But the second season their weight increased remarkably in relation to the very high total. They alone furnished 69 percent. Yield of forbs was originally small and averaged only about 6 percent of the total. This decreased to half the second year, a loss even greater than that sustained by the pasture grasses.

These data show clearly the trend in succession and something of its time relations. It would appear that if left undisturbed except by autumnal mowing, this rapidly degenerating prairie would soon be dominated again by native grasses. Bluegrass and weeds would be replaced almost completely by these and native prairie forbs.

SUMMARY

This study describes the late stages of succession in two subseres areas (I & II) in true prairie near Lincoln, Nebraska.

I. The first prairie area, after many years of grazing followed by several years of drought (1934-36), had degenerated so that when it was exclosed to livestock in 1937, prairie grasses occurred only sparingly and bluegrass remained only in patches. The first part of this study describes the late stage of stabilization in the pasture in 1948-49.

Large samples of the vegetation of the subere and of the adjacent contiguous prairie from which it originated were mapped and compared as to composition and structure.

A little bluestem type occupied the upper third of the north-facing slope; big bluestem type had developed on mid-portion; and a big bluestem-Kentucky bluegrass type was found on the deeper and richer soil of the nearly level lower third of the subere.

Little bluestem was sparse throughout, but it was more than three times as abundant in prairie as in pasture. Big bluestem in the little bluestem pasture type occurred sparingly and mostly in small bunches. Elsewhere, there was almost as much of this grass in pasture as in prairie. Bluegrass was abundant and widely scattered in pasture, and always present but sparse in prairie. Blue grama occurred only in pasture and side-oats grama was more abundant there. Tall dropseed was abundant in prairie but rare in pasture. Sand dropseed occurred throughout the pasture where it invaded during the drought. It was not found in prairie. Forbs were not abundant in the subere, even eight years after the drought, despite their large variety and abundance in the prairie.

The average air dry yield of prairie grasses (1948-49) was 24 percent greater in prairie, but pasture grasses yielded 60 percent less than in the subere. The yield of forbs was 120 percent greater in prairie.

Although the soil was fully occupied and a good mulch was re-established, the regular cover of climax prairie did not prevail and the understory was poorly developed. A period of many good years will yet be required for dynamic stabilization and the completion of succession.

II. In the second subere, regeneration of native grasses was studied in a low-land prairie which, under grazing, had degenerated into an almost pure

stand of bluegrass. Permanent exclosures were established in early spring of 1948, and the development of any relict vegetation in them was compared with similar relicts outside under year-long grazing.

Stems of big bluestem in the exclosures had increased in 1949 more than fourfold, compared with a 16 percent decrease in the pasture. Its regained vigor was shown by the production the second year of 742 flower stalks of normal stature compared with only 28 weak ones the first year. Similar increase in stems of little bluestem were more than eightfold. Needlegrass also recovered rapidly.

The first year, pasture grasses (mostly bluegrass) in the exclosures furnished 48 percent of the total yield; the second year only 28. Prairie grasses composed only 46 percent of the total yield the first year but 69 the second. Due to the recovery of prairie grasses, total plant production in 1949 far exceeded any increase due to difference in seasonal environment.

Under protection, a strong successional trend had begun which would eliminate nearly all bluegrass and weeds and rapidly restore a near-climax or climax vegetation.

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CONTENTS

July, 1951

- Forrest Shreve, 1878-1950.....H. L. Schantz
Interrelations of certain physical and chemical features in a headwater
limestone stream.....Joe Kendall Noel
A functional, factorial approach to plant ecology.....Jack Major
The autotrophon; an apparatus for rearing insects under controlled
conditions with automatic time-controlled withdrawal of samples.....John Stanley
The return of native perennial bunchgrass following the removal of Klamath weed
(*Hypericum perforatum* L.) by imported beetles.....Carl B. Huffaker
The relation between level of population and pregnancy of Norway rats.....David E. Davis
The relation between level of population and size and sex of Norway rats....David E. Davis
The relation between the level of population and the prevalence of *Leptospira*,
Salmonella, and *Capillaria* in Norway rats.....David E. Davis
A comparison of reproductive potential of two rat populations.....David E. Davis
An upland forest continuum in the prairie-forest border region of Wisconsin
J. T. Curtis and R. P. McIntosh
Clutch-size and egg mortality of Kent Island eiders.....Raymond A. Paynter, Jr.
Vegetation mapping as a guide to better silviculture.....Marinus Westveld
Pollen succession in the sediments of Singletary Lake, North Carolina.....David G. Frey
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